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NOTE.—Slight errors have been corrected in the Index.

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- 14, line 23, for *cephalocypha* read *cephaloscyptha*.
 45 „ 20 „ TRIBULOIDES „ TRIBULOIDES.
 50, last line, for *obtusa* read *obtusula*.
 77, line 24, for STELLUTATA read STELLULATA.
 227 „ 36 „ NIEWENHUIJSE „ NIEWENHUIS.
 313, Title, for Great Britain read Britain.
 „ line 1, for Hack. read Linn.
 314 „ 12 „ o „ to.
 „ „ 35, read (Hegets. & Heer).
 „ „ 36 „ (Linn.).
 „ „ 38 „ (Osb.).
 319 „ 12, for “subvar. *arenaria*” read “var. h. *arenaria*.”
 320 „ 29 „ “subvars. *grandiflora*” „ “vars. *grandiflora*.”
 „ „ 42 „ “Subvar. *barbata*” „ “var. *barbata*.”
 331, Plate 26, fig. 3, read “subsp. *fallax*.”
 fig. 4 „ “subsp. *genuina*.”
 figs. 1, a-h, read “var.” in place of “subvar.”
 335, line 2, for *truncicolum* read *truncicola*.
 358, Explanation of Plate 32, for $\times 2.4$ read $\times 1.46$.
 „ $\times 50$ „ $\times 30.6$
 „ $\times 25.5$ „ $\times 15.6$.
 358, Explanation of Plates 33 & 34, for $\times 2.4$ read $\times 1.3$.
 „ $\times 50$ „ $\times 27$.
 „ $\times 25.5$ „ $\times 13.8$.
 „ $\times 27$ „ $\times 14.6$.
 363, line 18, for *erythrogona* read *erythrogyna*.
 373, after line 28, insert: Recorded by Braun from Bengal.
 391, line 21, for “the portion” read “a portion.”
 397 „ 34, „ “Valcimira” „ “Valcimara.”
 399, last line but one, for “Sibley’s” read “Sibthorp’s.”
 413, line 13, for “stomata are” read “water is.”

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The Heleoplankton of three Berkshire Pools.
By B. MILLARD GRIFFITHS, M.Sc. (Birm.), F.L.S.

(PLATE 1.)

[Read 16th March, 1922.]

IN August 1910, a survey was made of nine pools in North Worcestershire with a view to ascertaining the plankton contents of relatively small bodies of water (Griffiths, 1912, 1916). The largest pool did not exceed eighteen acres in area, and the smallest was less than one acre.

The following work is a continuation of this type of investigation, and it is hoped to extend the survey over the lowland areas of the British Isles. Little work has been done on the heleoplankton of this country, although the larger lakes of the northern and western areas have been extensively studied.

During June and July 1920, three pools were examined in the neighbourhood of Reading, Berks. The largest pool was twenty-three acres in area and the smallest seventeen. In every case the pools have been artificially constructed by the laying down of dams across stream-valleys. The pools are all situated in extensive private estates, and are used only for fishing and shooting. They lie at an elevation of about 180 feet O.D., in the relatively flat district between the rivers Kennet and Loddon. They are all headwaters, and receive their supply from low elevations little more than 200 feet in height. The two Bulmershe pools drain to the Loddon, but Whiteknights

drains to the Thames. The overflow streams are of small volume, and their courses are for the most part through drainage ditches. The soil is London Clay.

Description of the Pools :—

1. Bulmershe North Pool.

Area about seventeen acres. Depth about ten or twelve feet over the larger area. Banks covered with tall trees and a thick undergrowth of *Rhododendron*. A small stream enters at the top end. Sides of the pool fringed with large masses of *Equisetum limosum* and some *Nymphaea alba*; on the bottom much *Myriophyllum*, and in some places *Polygonum amphibium*. Water dark in colour and opaque, owing to quantity of plankton. Middle of pool free from weeds. Temperature of water six inches below the surface, 18 deg. C.

2. Bulmershe South Pool.

Area about twenty-three acres. Pool much broader than the former and not so much shaded by trees. Banks covered with thick growth of *Rhododendron*, with trees some distance behind. At the upper end is park-land extending back to the mansion. Depth of water about six to ten feet over the larger area but shallower towards top end, where considerable masses of *Polygonum amphibium* and *Ranunculus aquatilis* occur. Water clear. At the south-west angle there is a small sphagnum bog. Temperature, 18 deg. C.

3. Whiteknights Pool.

Area about eighteen acres. Pool elongated. Banks of pool lined with tall but not densely crowded trees; the dam lined with pollard willows. Sides of pool fringed with broad sheets of *Nymphaea alba*; middle completely free from weeds. Depth about twenty feet or more in middle, and the sides rapidly shelving. Water brownish in colour and opaque, owing to quantity of plankton. Temperature, 20 deg. C.

The water-supply of all the pools is from bottom springs and from park-land, and it is probably entirely free from contamination either from arable land or from house-drainage. In no case does a strong stream enter, and the outflows are small. The two Bulmershe Pools are separated by only a few hundred yards of woodland. Whiteknights Pool lies about a mile west of Bulmershe South Pool.

The collections of plankton were taken by means of a fine silk net, six inches in diameter and eighteen inches long, towed behind a boat at a depth of a few inches below the surface. The course of the boat was along the middle of the pool, where weeds were absent.

List of Algae.

ccc=abundant, cc=common, c=fairly common, r=few, rr=rare, rrr=very rare.	Bulmershe North Pool.	Bulmershe South Pool.	Whiteknights Pool.
Temperature in °C.	18	18	20
CHLOROPHYCEÆ.			
<i>Pandorina morum</i> (Müll.), Bory	cc
<i>Eudorina elegans</i> , Ehrenb.	cc	
<i>Volvox aureus</i> , Ehrenb.	c	
<i>Pediastrum duplex</i> , Meyen	rrr	..	r
" <i>tetras</i> (Ehrenb.), Ralfs.	rr	
<i>Crucigenia rectangularis</i> (Naeg.), Gay ..	r	c	
" <i>Tetrapedia</i> (Kirchn.), W. & G. S. West	rr
" <i>minima</i> (Fitschen), Brunnthaler	rr
<i>Scenedesmus quadricauda</i> (Turp.), Bréb.	r
" <i>bijugatus</i> , var. <i>arcuatus</i> (Lemm.), G. S. West. .	rrr	..	
<i>Ankistrodesmus falcatus</i> (Corda), Ralfs.	c	
<i>Kirchneriella obesa</i> (West), Schmidle	r	
<i>Oocystis parva</i> , W. & G. S. West	rr	
" <i>solitaria</i> , Witttr.	r	
<i>Nephrocytium obesum</i> , West	rr	
<i>Tetradron minimum</i> (A. Br.), Hansg.	c	
" <i>trigonum</i> (Naeg.), Hansg.	r	
" <i>muticum</i> (A. Br.), Hansg.	c
" <i>hastatum</i> , var. <i>pulatinum</i> (Schmidle), Hansg.	r
" <i>regulare</i> , Kütz., var. <i>Incus</i> , Teiling	r
<i>Lagerheimia wratislaviensis</i> , Schroeder	rr
<i>Dictyosphaerium pulchellum</i> , Wood.	c	rr	rrr
<i>Sphaerocystis Schroeteri</i> , Chodat	r	..	
<i>Glæocystis gigas</i> (Kütz.), Lagerh.	r	
<i>Closterium aciculare</i> , T. West, var. <i>subprorum</i> , G. S. West. .	..	ccc	
<i>Pleurotæmium Trabecula</i> (Ehrenb.), Naeg.	r	
<i>Euastrum verrucosum</i> , Ehrenb., var. <i>coarctatum</i> , Delp.	rrr	
<i>Microsterias papulifera</i> , Bréb.	rrr	
<i>Cosmarium abbreviatum</i> , Racib.	rrr	
" <i>bioculatum</i> , Bréb.	rr	
" <i>Phaseolus</i> , Bréb.	c	
" <i>turgidum</i> , Bréb.	rrr	
" <i>margaritifera</i> , Menegh.	rrr	
" <i>ovale</i> , Ralfs.	rrr	
" <i>Meneghinii</i> , Bréb.	cc	
<i>Xanthidium antilopeum</i> (Bréb.), Kütz.	c	
<i>Artthrodesmus bifidus</i> , Bréb., var. <i>truncatus</i> , West	rr	
<i>Stauroastrum Bienianum</i> , Rabenh.	c	
" <i>alternans</i> , Bréb.	rr	
" <i>cuspidatum</i> , Ralfs.	rrr	
" <i>furcigerum</i> , Bréb.	rrr	
" <i>teliferum</i> , Ralfs.	rr	..	

List of Algae (contd.).

ccc=abundant, cc=common, c=fairly common, r=few, rr=rare, rrr=very rare.	Bulmershe North Pool.	Bulmershe South Pool.	Whiteknights Pool.
Temperature in ° C.	18	18	20
CHLOROPHYCEÆ (cont.).			
<i>Desmidiium Schwartzii</i> , Ag.	r	
<i>Sphaerosoma</i> sp.	rr	
<i>Radiolium conjunctivum</i> , Schmidle	rr	
<i>Geminella interrupta</i> , Turp.	r	
HETEROKONTÆ.			
<i>Tribonema affine</i> (Kütz.), G. S. West	ccc	..	c
BACILLARIEÆ.			
<i>Rhizosolenia longisetu</i> , Zach.	r
<i>Synedra Acus</i> , Kütz.	ccc
<i>Cyclotella Kuetzingiana</i> , Thwaites	c
<i>Stephanodiscus Hantzschianus</i> , Grun.	r
MYXOPHYCEÆ.			
<i>Microcystis æruginosa</i> , Kütz.	r	
<i>Aphanothece microscopica</i> , Naeg.	r	
<i>Aphanocapsa delicatissima</i> , G. S. West	..	c	
<i>Grevillei</i> (Hass.), Rabenh.	rr	
<i>Nodularia sphaerocarpa</i> , Born. & Flah.	rr
PERIDINIEÆ.			
<i>Glenodinium uliginosum</i> , Schilling	rrr	
<i>Peridinium Willei</i> , Huittf.-Kaas.	cc	cc	
<i>cinctum</i> , Ehrenb.	c		
<i>anglicum</i> , G. S. West	rr	..	c
<i>bipes</i> , Stein, and var. <i>excisum</i> , Lemm.	c	c	
<i>inconspicuum</i> , Lemm.	c	
<i>Suttoni</i> , sp. nov.	cc
<i>Ceratium Hirundinella</i> (O. F. Müller), Schrank, 3 h.	ccc	..	ccc
" " " " 2 h.	ccc	
DINOBRYACEÆ.			
<i>Dinobryon Sertularia</i> , Ehrenb.	ccc		

THE ALGA-FLORA.

The marked individuality of planktons noticed in the pools of North Worcestershire (Griffiths, 1916) was found to hold in the case of the Berkshire pools. The planktons are so different that a single glance under the microscope is sufficient to distinguish them from each other.

The dominant plankton constituents, arranged in order of abundance, are as follows :—

1. Bulmershe North Pool. *Ceratium Hirundinella* (three-horned form), *Tribonema affine*, *Dinobryon Sertularia*, *Peridinium Willei*, *P. cinctum*, *P. bipes*, *Dictyosporium pulchellum*.
2. Bulmershe South Pool. *Ceratium Hirundinella* (two-horned form), *Closterium aciculare* var. *subpromum*, *Peridinium Willei*, *Eudorina elegans*, *Cosmarium Meneghinii*, *Peridinium bipes*, *Volvox aureus*.
3. Whiteknights Pool. *Ceratium Hirundinella* (three-horned form), *Synedra Acus*, *Peridinium Suttoni*, *Pandorina morum*, *Peridinium anglicum*, *Tribonema affine*, *Cyclotella Kuetzingiana*.

It will be seen from the above table that the most abundant organisms of the plankton are the Peridiniæ, no less than eight species being present in the three pools. In this respect the pools differ from those of North Worcestershire, but resemble that of Bracebridge Pool, Warwickshire (West, 1909 ii.). One species, *P. Suttoni*, occurring abundantly in Whiteknights Pool, is new, and *P. Willei*, found in quantity in the two Bulmershe pools, has not been recorded previously for small lowland pools. *P. Willei* closely resembles *P. cinctum*, with which it was associated in Bulmershe North Pool. *P. anglicum* was originally described from Bracebridge Pool, and it also occurred in Stanklin Pool, Wores. (Griffiths, 1912, 1916). It formed a considerable proportion of the plankton of Whiteknights Pool, in association with *P. Suttoni*.

In every pool the bulk of the plankton consisted of *Ceratium Hirundinella*. The form with three basal horns occurred in both Bulmershe North and Whiteknights, but the two-horned form was confined exclusively to Bulmershe South. The two three-horned forms were not absolutely identical. It is notable that the two Bulmershe pools, in spite of their close proximity, contained entirely distinct forms of the organism, whereas the more distant Whiteknights had a form practically identical with that of Bulmershe North.

Peridinium bipes occurred in both Bulmershe pools, and in each instance included the type-form together with the variety *excisum*.

Peridinium inconspicuum has been found previously in Bracebridge Pool. It was fairly frequent in Bulmershe South.

Glenodinium uliginosum was found in very small numbers in Bulmershe South, but its condition indicated that it was probably a mere casual from the small sphagnum bog near the south-west corner of the pool.

A striking feature of the plankton is the very small number of Myxophyceæ present. Only five species were found, and none were in any quantity. The Bacillariæ are also very poorly represented by four species, but one of these, *Synedra Acus*, occurred in quantity in Whiteknights Pool. The paucity of these groups may be due to the absence of contamination of the water by house-drainage or by drainage from arable land.

The dominance of *Tribonema affine* in Bulmershe North Pool is a peculiar feature, as its usual habitat is in ditches etc. Species of this genus appear to become temporary plankton forms occasionally. *Tribonema minus* (Wille), Hazen, is recorded as suddenly appearing in the plankton of Lake Mendota, Wisconsin (Smith, 1920), and *T. bombycina* forma *depauperata*, Wille, occurs in some of the Danish lakes (Wesenberg-Lund, 1908). *T. affine* is also given as occurring in some of the Scotch lakes (West & West, 1909). In the case of the Berkshire pools, the distribution is peculiar, for the organism is absent from the adjacent Bulmershe South Pool and present in the more distant Whiteknights.

The Desmids are represented by some twenty species—nineteen in Bulmershe South, one in Bulmershe North, and none in Whiteknights. Most of them were found in very small numbers, and they are most probably derived from the small sphagnum bog or from the weeds. In the case of *Osterium aciculare* var. *subpronum*, however, we probably have a true plankton desmid. It formed a considerable part of the plankton of Bulmershe South Pool, associated with *Xanthidium antilopeum*, which, though not in great abundance, was in a healthy and dividing condition. *Staurastrum teliferum* was the sole desmid found in the neighbouring Bulmershe North Pool, but only in very small numbers.

Of the other important plankton organisms, *Pandorina morum* was confined to Whiteknights, and *Eudorina elegans* and *Volvox aureus* were confined to Bulmershe South. The Flagellate, *Dinobryon Sertularia*, was very plentiful in Bulmershe North, where also *Dictyosphaerium pulchellum* attained some importance. The latter alga was the sole form common to all three pools.

The above account shows that the planktons even of adjacent pools are very dissimilar. The causes of the differences are very obscure, for though it has been shown by West and West (1900) that, in general, dominant desmid planktons are associated with "purity" of water, the factors determining the distribution of other organisms are practically unknown. In the case of the Berkshire pools, their situation on similar subsoils, in closely similar environments and in close proximity, does not prevent the most

marked differences in the contents of their planktons. It will be seen that the adjacent Bulmershe Pools have only four species in common, whereas Bulmershe North and Whiteknights have five species in common and Bulmershe South and Whiteknights only one. Thirty-eight out of the forty species found in Bulmershe South are confined to that pool, five out of thirteen to Bulmershe North, and fourteen out of nineteen to Whiteknights.

The causes of the distribution are doubtless complex in any case, but the complexity will be even greater in a small pool than in a large lake. Assuming that the main factor is the nature of the substances dissolved in the water, it follows that the variations in the composition and concentration of the solution will depend mainly on the volume of water in the pool or lake. For in the first place, any given depth of rainfall will dilute the bulk of a large lake much less than the same depth of rainfall would that of a small pool. The drainage also, bringing in dissolved substances, will have a much smaller effect on the composition of the large volume of water in a lake than on the lesser volume in a pool. Furthermore, the fringe of aquatic vegetation will materially alter composition of the water by the withdrawal of substances necessary for growth and by the addition of the products of decay; and as the weed-fringe of a small pool is relatively greater in proportion to the bulk of water than in the case of a lake, the smaller body of water will undergo greater variations in the nature of the substances in it.

In a small pool, therefore, slight differences in the volume of water, or in the size and nature of the drainage of the area, or in the amount of kind of aquatic vegetation, will exercise a relatively great effect on the composition of the water solution. It is therefore not surprising that the planktons of small pools should differ from one another to the extent they do.

Whatever the chemical effects of the aquatic vegetation may be, what one might call the ecological effects are all important in the case of the smaller bodies of water. The algæ collected by the plankton net are in the majority of cases not permanent denizens of the surface water, but are derived from the benthos. Their true habitat is among the leaves of the macrophytic aquatic vegetation or in the mud of the shallower parts, and they are carried out by the agitation of the water by the wind. They mingle with the true planktonic algæ for a time, but as they have no devices with which to counteract the pull of gravity, they soon sink below the region of minimum photic action and perish.

Of the algæ shown in the list, only the Peridiniæ (except *Glenodinium uliginosum*), the Volvocaceæ, and perhaps the two desmids (*Closterium ariculare* and *Xanthidium antilopeum*) may claim to be planktonic. The rest are from the benthos, even though they may be in large numbers. It is clear, therefore, that the plankton of a small pool is to a large extent dependent on the presence of aquatic vegetation; and as it is possible that different species

of aquatics may harbour different communities of algæ, the various plant-associations met with in small pools will again tend to accentuate the differences in the planktons.

SPECIES OF SPECIAL INTEREST.

1. PERIDINIUM WILLEI, Huitf.-Kaas., West, Algæ 1916, p. 62.

This Peridininian occurred plentifully in the two Bulmershe pools. In the South Pool it occurred alone, but in the North Pool it was associated with *P. cinctum*. It is widely distributed in the larger lakes of the British Isles (West & West, 1909), but it has not been found in any of the Worcestershire or Warwickshire pools. Its occurrence in a relatively small pool is therefore of some interest. *P. Willei* resembles *P. cinctum*, differing mainly in the shape of the third apical intercalary plate and in the slight median asymmetry of the plates of the hypovalve. It also closely resembles *P. Volzii*, Lemm., var. *australe*, G. S. West (West, 1901 i.), the chief difference being in the even more marked asymmetry of the hypovalve of the latter. The diagram of the plates of *P. Willei*, given in the 'Süsswasserflora,' Heft 3, p. 45, fig. 51, differs considerably from that given by West. The identification has been made from West's figures, as they seem less diagrammatic than the others.

2. PERIDINIUM SUTTONI, sp. nov. (Pl. 1. figs. 1-6.)

This species formed one of the dominant constituents of the plankton of Whiteknights Pool. It appears to differ from any species previously described. The epivalve is more or less conical and slightly longer than the hypovalve. The latter is hemispherical and provided with short, stout spines. Using the nomenclature of Kofoid (see West, Algæ, 1916, p. 15), the structure of the cell-wall is as follows:—

The plates of the epivalve comprise 6 precingulars, 4 apicals bounding the somewhat elongated pore, and 1 pentagonal apical intercalary plate surrounded by 2'', 3'', 4'' and 2', 3' (Pl. 1. figs. 3, 5). The hypovalve is medianly symmetrical, consisting of 5 postcingulars and 2 equal antapicals (figs. 4, 6). Each of the postcingular plates except No. 3, and both the antapical plates, bear one broad-based conical spine more or less centrally placed. Occasionally there are two spines on each antapical plate and none on the Nos. 2 and 4 postcingulars (fig. 6).

All the plates are minutely punctate. Intercalary bands may develop between the plates, but as a rule those between the apical plates remain narrow. There is an elongated and sinuous flagellar pore in the ventral groove.

Most of the specimens were either empty or their contents were aggregated into cysts. The alga is therefore most probably an early summer

form, and the collection was taken at the end of its phase. The associated *P. anglicum* was in the same condition.

The species has been named after the family of Sutton, whose name is closely associated with the Reading district, and whose contributions to horticultural and agricultural botany are well known.

DIAGNOSIS. *Peridinium Suttoni*, sp. nov. ; corpore in partibus inæqualibus duabus a fossa transversa diviso, parte apicali vel anteriori conicali, parte inferiori vel posteriori semisphericali ; fossa transversa æquatoriale disposita.

Epivalva e tabulis 11 composita ; tabulis præcingularibus 6, tabulis apicalibus 3, tabula intercalaria 1.

Hypovalva e tabulis 7 composita ; tabulis antapicalibus æqualibus 2, uni vel duobus spinis conicalibus ornatis ; tabulis posteingularibus 5, e quibus 4 plus vel minus medialibus spinis conicalibus ornatae sunt. Tabulae punctulatae delicatissimae.

3. PERIDINIUM BIPES, Stein, and var. EXCISTUM, Lemm.

The type-form and the variety occurred together in both the Bulmershe Pools. The type-form was much less numerous than the variety. The specimens also were more tumid and less attenuate than is shown in the figure given in the *Süsswasserfl.*, H. 3, p. 36. Occasionally forms were found in which the basal spines were dentate (see Pl. 1. fig. 7).

4. RHIZOSOLENIA LONGISETA, Zach.

The diatom was found in very small numbers in Whiteknights Pool. It occurs in the plankton of some of the Scottish lakes and in pools on the Continent, but it is an uncommon alga. Three specimens are figured (Pl. 1. fig. 9) to show variations in size.

5. STEPHANODISCUS HANTZ-SCHIANUS, Grun. (British F. W. Algae, G. S. West, 1904, fig. 127 A, p. 277).

This diatom also occurred in Whiteknights Pool in very small numbers associated with *Cyclotella Kuetzingiana* and *Synedra acus*. It has been recorded in the British Isles from Lough Neagh, and is a distinctly rare alga.

6. LAGERHEIMIA WRATISLAVIENSIS, Schroeder. (Pl. 1. fig. 8.)

The alga occurred in very small numbers in Whiteknights Pool. It is distinguished from similar species by the position of the spines, which are placed in alignment with the major and minor axes of the cell. It is recorded twice for the English Midlands (Grove, 1920, p. 27), and it is a sporadic constituent of Continental pools, but is not commonly found.

7. CRUCIGENIA TETRAPEDIA (Kirchn.), W. & G. S. West. (Pl. 1. fig. 11.)

This organism was found in very small numbers in Whiteknights Pool. Only colonies of four cells were seen. It is recorded from the plankton of Lough Neagh and from that of the Oder.

8. *CRUCIGENIA MINIMA* (Fitschen), Brunnthaler. (Pl. 1. fig. 12.)

This minute species also occurred in very small numbers in Whiteknights Pool. It resembles *Tetrastrum staurogenieforme*, but differs from it in the complete absence of spines and the smaller size and the looser arrangement of the cells. It has not been recorded previously for this country.

9. *RADIOFILUM CONJUNCTIVUM*, Schmidle. (Pl. 1. fig. 10.)

The alga was found in small quantities in Bulmershe South Pool. The mucous investment is exceedingly delicate and transparent. The median transverse lines of the cell are distinctly seen. Colonies consisting of as many as fifty cells occur, but in most cases the number is about half that. The alga has been recorded for the South of Europe and for Australia, but it has not previously been found in this country.

10. *CERATIUM HIRUNDINELLA* (O. F. Müller), Schrank.

Each of the pools had its own form of this very variable species. The three-horned form occurred in Bulmershe North Pool and in Whiteknights, but the two forms were not absolutely identical. In Bulmershe South Pool the two-horned form was found. In each case the particular form was present without any intermixture with the other.

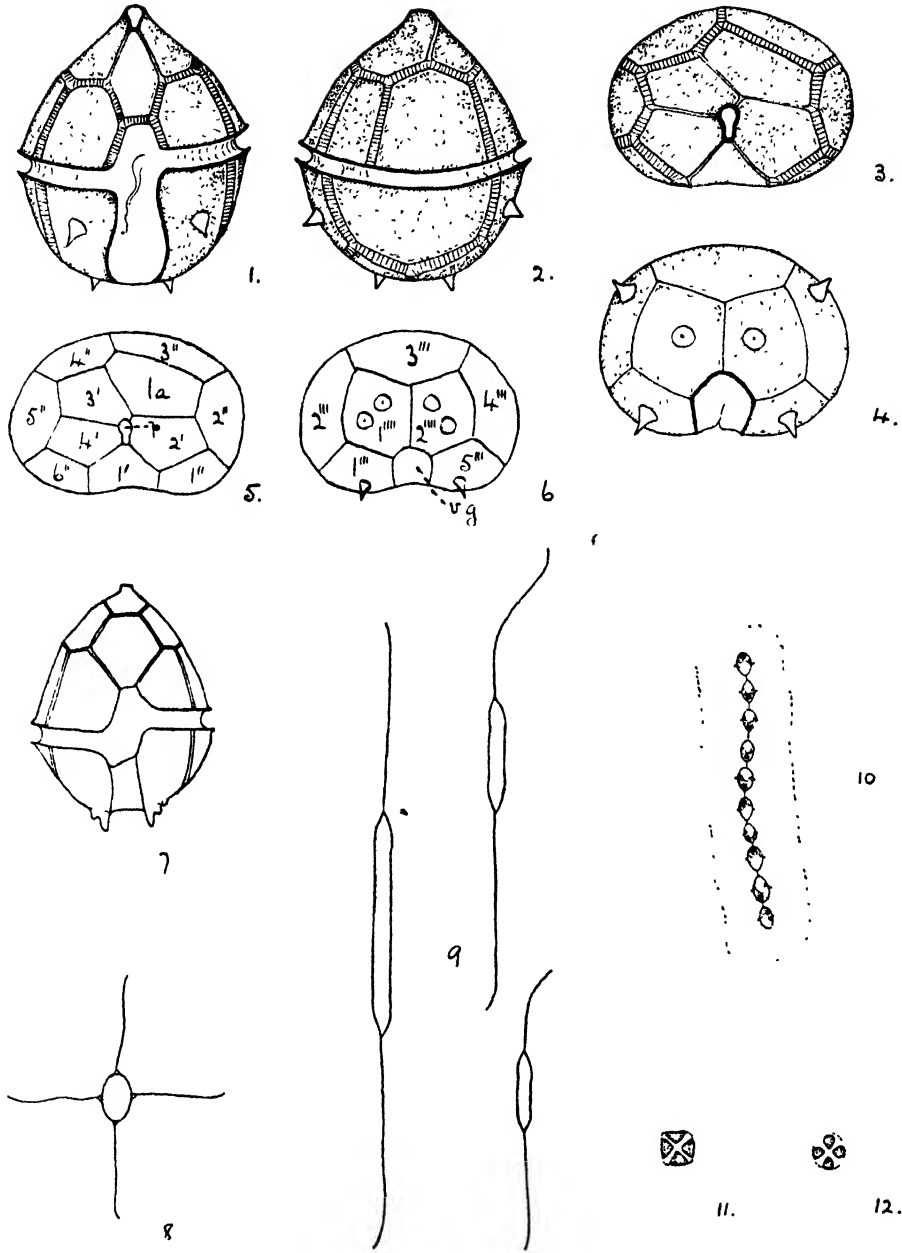
In conclusion, I wish to thank Mr. J. Rushbrook of Bulmershe Court for his kind permission to collect from Bulmershe Pools, and Mr. Guy Hargreaves of Whiteknights Park, and Mr. Hearst of Foxhill for permission to collect from Whiteknights Pool. I should like also to thank Mr. L. Sutton and Mr. M. H. F. Sutton for their help regarding the latter pool.

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May, 1921.

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DESCRIPTION OF PLATE 1.

- Fig. 1. *Peridinium Suttoni*: ventral view. × 1200.
2. „ „ dorsal view. × 1200.
3. „ „ apical view. × 1200.
4. „ „ antapical view. × 1200.
- 5 & 6. Diagrams of plates of valves: 1'-4', apicals; 1α, apical intercalary; 1''-6'', pre-cingulars; p., apical pore; 1'''-5''', postcingulars; 1''''-2''''', antapicals; v.g., ventral groove.
7. *Peridinium bipes*: ventral view of form with dentate spines. × 650.
8. *Lagerheimia wratislaviensis*. × 650.
9. *Rhizosolenia longiseta*: three specimens. × 650.
10. *Radiofilum conjunctivum*. × 650.
11. *Crucigenia Tetrapedia*. × 650.
12. „ *minima*. × 650.

A Systematic Account of the Plants collected in New Caledonia and the Isle of Pines by Mr. R. H. COMPTON, M.A., in 1914.—PART III. Cryptogams (Hepaticæ—Fungi). (Communicated by Dr. A. B. RENDLE, F.R.S., Sec.L.S.)

HEPATICÆ.

By WM. H. PEARSON, M.Sc., A.L.S.

(PLATES 2, 3.)

[Read 4th March, 1920.]

A CONSIDERABLE number of Hepatics have previously been collected in New Caledonia by Balansa, Buss, Deplanche, Étesse, Franc, Germain, M. & Mme. Lerat, Sarazin, Savès, and Viillard; these have all been named by Stephani, with the exception of three by Bescherelle & Spruce; these are all recorded in Stephani's 'Species Hepaticarum.'

Most of the species published are endemic; many of these have been collected by Prof. Compton; and the numerous new species in the following list are also endemic.

They are all closely related either to those of Malaya or Australia. I have no desire to add to the list of new species, but where I have not been able to allocate the plant to any species already described, or to find it to agree with any of Stephani's species which I have seen, I have described it as new. I am vain enough to think that if any of my supposed new species have already been published by Stephani, my full descriptions will enable future students to be better able to identify those published by Stephani, whose descriptions are in some cases very short and vague. I use the relative terms for size of plants and cells as adopted by Dr. Spruce.

I refuse to adopt Trevisan's generic name in place of Spruce's *Acrolejeunea*, and can give good reasons for doing so.

Through the kindness of Prof. Lesage, of Rennes, I have had the opportunity of comparing my specimens with many of Stephani's originals, which has been of great assistance to me; my thanks are due to him; also to Mr. A. Gepp for his valued help in translating my descriptions into Latin and for other assistance.

PLAGIOCHASMA BISETULUM St., Sp. Hep. Suppl. vi. 6, 1917.

Obs. Stomata large, surrounded by six large cells; squamæ purple; appendages bi-setulose.

Endemic.

Hab. Mont Mou. On stones and mud, by stream. 479.

DUMORTIERA NEPALENSIS (Tayl.), Nees, Nat. Eur. Leberm. iv. 169, 1838.

Hygropyla nepalensis Tayl. in Trans. Linn. Soc. xvii. (1836) 392, pl. 15. f. 2.

Marchantia trichoccephala Hook. Ic. Pl. pl. 158, 1837.

Dumortiera hirsuta latior Gottsche, Lindenb. & Nees, Syn. Hep. 544, 1846.

Dumortiera hirsuta trichopus Spruce in Trans. Bot. Soc. Edinb. xv. (1885) 587.

Dumortiera velutina Schiffn. in Denkschr. Math.-Naturw. Cl. Kais. Acad. Wien, lxvi. 156, 1899.

Dumortiera calcicola Campbell in Ann. Bot. xxxii. (1918), pl. 8. f. 9.

(Obs. Prof. Alexander W. Evans, in his latest paper on the genus *Dumortiera* (Bull. Torrey Bot. Club, xlv. (1919) 167-188), reduces all the known species of this genus to two, *D. hirsuta* (Sw.) and *D. nepalensis* (Tayl.), the former with a smooth antical surface, the latter with a papillose one; all Prof. Compton's specimens belong to the latter.

The list of synonyms is taken from Prof. Evans's admirable paper.

Hab. Ermitage Stream. On rocks in spray of waterfall. 180. Mont Canala. High forest, 900 ft. 1138. Mont Canala. On rocks by stream in deep shade, 1500 ft. 1184.

MARCHANTIA BERTEROANA Lehm. & Lindenb.; Lehmann, Pug. Plant. vi. (1834) 21.

Marchantia tabularis Nees, Naturg. Europ. Leberm. iv. (1838) 71 (foot-note).

Marchantia cephaloscypha Steph. Hedwigia, xxii. (1883) 51.

Prof. Alexander W. Evans, in his paper "The American Species of *Marchantia*" (Trans. Conn. Ac. vol. xxi. 1917), has some useful notes on Exotic *Marchantia*. He reduces *M. tabularis* Nees and *M. cephaloscypha* St. to synonyms of *Berteroana* Lehm. & Lindenb. I sent him specimens of Prof. Compton's No. 1807, and he writes:—"I am much interested in *Marchantia* from New Caledonia. I think that it represents *M. Berteroana*, and the occurrence of this species in New Caledonia would not be surprising when we keep in mind its wide distribution in the Southern Hemisphere. It seems to me that the appendages in your plant are not absolutely entire, but that they show faint crenulations here and there, and I have seen appendages similar to yours in material from other localities. I am afraid my descriptive phrase, as you imply, is a little misleading. I did not mean to suggest, however, that every marginal cell projected in all cases, but that projecting cells could be found on practically all appendages. It would have been better if I had brought out this idea more clearly." The appendages of Prof. Compton's plant are, generally speaking, quite entire, marginal cells minute, the cupules acutely lobate, each lobe terminating in a

long, straight, or hamate cilium, with the margin of the lobes fringed with short spines; cupules very large and high, exterior surface papillose. I have not had the opportunity of comparing it with specimens of *M. Berteroana*.

Hab. Mont Panic. Spreading over burnt wood in forest, 1500 ft. 1807.

Distrib. Cape of Good Hope, Transvaal, St. Helena, Australia, Tasmania, New Zealand, Fuegia, Patagonia, Chile.

MARCHANTIA LECORDIANA St., Sp. Hep. in Bull. Herb. Boissier, vii. (1899) 525.

Medium size; pale yellowish green in colour. Fronds simple, lobate, furcate or bifurcate, regular, narrow, plano-convexulous; antical side flat, postical slightly convex, at the middle 20 small cells thick, with a few larger ones interspersed. Stomata numerous, regularly or irregularly dispersed, clear, with no projecting interior cells, 3 tiers high of 4 barrel-shaped cells. Cupules small, mouth wide, spreading, not lobate, very shallow, margin dentate-spinulose, teeth 1 to 3 cells long, 2 cells wide at the base, exterior of walls verruculose. Scales oval, entire, or with a few very minute distant teeth; appendages small, purple, reflexed, constricted at the base, reniform, orbicular or ovate, apex acute, margin dentate, with 10 to 12 teeth. Rays of male flowers 7, cuneate, apex retuse.

Dimensions. Fronds 1 to $1\frac{1}{2}$ inch long, 5 mm. to 7.5 mm. wide; scales 1 mm. \times .5 mm.; appendages .4 mm. \times .3 mm., .3 mm. \times .25 mm.

Obs. As noted by Prof. Evans, the appendages to the scales afford an excellent character for discriminating the species of *Marchantia*.

In *M. Lecordiana* they are very characteristic. I have had the opportunity of comparing my specimens with the original specimens in the herbarium of the late Général Paris.

Endemic.

Hab. Mont Mou. On old tree stumps, in dense forest, 2200 ft. 450. Mont Arago. Abundant along stream side, in forest, 1000 ft. 1426.

ANEURA PULCRA Pearson, sp. nov. (Pl. 2. figs. 1-5.)

Dioica (?), mediocris rubello-brunnea stratificata. Frondes bipinnatæ; pinnæ et pinnulæ ascendentes patent-divergentes (70°) vel patentæ (50°) digitatæ flabelliformesve; caulis exalatus sectione transversâ ovalis biconvexus, angulis rotundatis, cellulas 6 crassus et 12 latus, cellulis periphericis 50 minutis; pinnæ pinnulæque oppositæ sub-oppositæve recurvatæ biconvexulæ alatæ, alis cellulas 2-3 latis, costâ cellulas 4 crassâ et 10 latâ. Flosculi feminei secus caulem utrinque dispositi, oppositi, bracteis immaturis laciniatis. Andrœcia haud visa.

Dimensions. Fronds 1 inch long; stems .6 mm. wide \times .4 mm. thick; pinnæ 3.5 mm. long; pinnulæ 1 mm. to 1.5 mm. long; pinnulæ .35 mm. wide \times .07 mm. thick; bracts .55 mm. high \times .4 mm. (explanate) wide.

Obs. The genus *Aneura* is not a particularly beautiful one, but this species is peculiarly striking and handsome.

A considerable number of species of *Aneura* are recorded by Stephani from New Caledonia, but none of those described by him agrees with this.

A. elegans is pale green, longer, regularly bipinnate, pinnæ 10 mm. long (in *A. pulchra* 3 mm.), stem .9 mm. \times .4 mm. (in *A. pulchra* .6 mm. \times .4 mm.), angles on both sides acute (in *A. pulchra* rotundate), pinnæ .67 mm. \times .17 mm. (in *A. pulchra* .35 mm. \times .07 mm.).

A. Leratii is autoicous, stem narrowly winged.

A. multispicata, brownish-green, flaccid, pinnæ 1.33 mm. \times .02 mm.

A. pembarensis, cross-section narrowly elliptical 1.17 mm. \times .025 mm.

A. plana, flaccid, pale brown, 1.67 mm. \times .25 mm.

A. subpalmata, stem 1.25 mm. \times .33 mm., pinnæ 1.33 mm. \times .25 mm.

A. valida, coriaceous, 1.33 mm. \times .58 mm.

A. venosa, of which only a very imperfect description is given by Stephani (Sp. Hep. Suppl. vi. 1917), has numerous long flagella; *A. pulchra* has none.

Hab. Ignambi. Matted coating on gneiss boulders in moist surroundings, 3000 ft. 1529.

ANEURA VIRIDISSIMA (Schiffner), St., Sp. Hep. 273, 1898.

Riccardia viridissima Schiffner in Denkschr. Kais. Ak. Wien, lxvii. (1898) 176.

Dioicous. Medium size; dark green in colour; caespitose. Stems simple or furcate, undulate, margin irregular; cross-section narrowly biconvex, 10 cells thick at the middle, gradually decreasing until 2 cells thick at the margin, no wings; 100 cells wide; cortical cells only slightly smaller than the inner. Calyptra smooth. No ♀ seen.

Dimensions. Stems 1 inch long, 5 mm. to 7.5 mm. wide, 1 mm. thick at the middle.

Hab. Ignambi. On rocks by creek, 3000 ft. 1530.

Distrib. Java.

ANEURA PLANA St., Sp. Hep. Suppl. vi. 38 (1917).

Var. MINOR Pearson, n. var.

Sterilis. Mediocris flaccida pallide brunnea irregulariter multi-ramosa, ramis exalatis pinnatis bipinnatisve; caulis sectione transversâ anguste biconvexus, 1.67 mm. latus \times 0.25 mm. crassus (cellulas 10 latus \times 4 crassus), cellulis periphericis 40 minimis, interioribus magnis hyalinis.

Obs. Agrees with the type (in herb. Général Paris), but is smaller.

Endemic.

Hab. Ignambi. Attached to stones under water, in running creek. Forest, 2000 ft. 1548.

ANEURA SUBPALMATA St., Sp. Hep. Suppl. vi. (1917) 43.

Dioicous? Small; dark yellowish-green in colour; densely imbricate cæspitose. Stems irregularly furcate, wingless, on cross-section oblong-biconvex, 5 to 6 cells thick at the middle, 20 cells wide, cortical cells very small, inner large, hyaline; branches as wide as stem, also wingless; texture very coriaceous; apices of branches retuse; immature ♀ bracts lacerate. Only young ♀ seen.

Dimensions. Stem $\frac{1}{2}$ to $\frac{3}{4}$ inch long, 1 mm. to 2 mm. wide, .3 mm. thick.

Obs. Agrees well with Stephani's description in its oblong-biconvex stem, minute cortical cells, large inner ones.

Endemic.

Hab. Ignambi. Forming dense coating over rocks by creek, moist forest, 2000 ft. 1547.

ANEURA COMPTONII Pearson, sp. nov.

Dioica, mediocris pallide Inteo-brunnea arcte cæspitosa. Caulis irregulariter ramosa lobata, lobis magnis et ambitu irregularibus, antico planus, postice convexulus, sectione transversâ linearis fere ad marginem usque æquicrassus, margine tenuiore cellulam 1 crassus, medio cellulas 6 crassus: cellulæ periphericæ paginæ posticæ c. 100 parvæ, interfores magnæ hyalinæ, duæ intimæ maximæ; textura firma coriacea; cellulæ periphericæ paginæ anticæ parvæ leptodermes, cellulæ subjacentes magnæ oblongæ hyalinæ parietibus firmis rubello-brunneis. Pagina postica rhizoideis crebris hyalinis obsita. Calyptra brevis cylindrica clavata, prope basin cellulas 8-10 crassus, cellulis periphericis 150 parvis, apice papillis c. 6 magnis conicis multicellularibus coronata; bractee basales 2 ovato-acutæ.

Planta mas amentula crebra brevia crassa gerens, alveolis in paria 3 dispositis, limbo antico laciniato.

Obs. Looks very like a *Pellia* in size and shape, and might easily be mistaken for that genus.

Although Stephani describes a number of species of *Aneura* from New Caledonia, I find none to which this species can be assigned; the coriaceous texture of the plant is one of its distinguishing characters.

Dimensions. Stems 1 to 2 inches long, 2 to 5 mm. wide, .2 mm. thick; calyptra 3 mm. long \times 1.25 mm. thick.

Hab. Mont Koghi. On stones and earth, in spray of cascade, 1000 ft. 755.

ANEURA MACRANTHA Pearson, sp. nov.

Monoica, mediocris luteo-viridis cæspitosa stratificata radiculosa. Frons firma simplex lobata vel furcata irregularis, margine integro, sectione transversâ plano-convexa, medio cellulas 12 crassa, utrinque sensim attenuata, margine cellulam 1 crassa. Squamæ ad calyptræ basin nullæ. Calyptra

maxima cylindrica lævis paulo clavata, medio cellulas 6 crassa, ore parvo, umbilicata.

Andrœcia ramis binis brevibus sita, alveolis in 3 paria dispositis. Capsulæ valvæ bistratæ, sectione transversâ cellulas quadratas, cellularum interiorum pariete exteriori crenulato, exhibentes. Sporæ verruculosæ fusco-brunneæ. Elateres angusti attenuati pallide lutei monospiri, spirâ 10-plo circumvolutâ.

Dimensions. Fronds 1 to $1\frac{1}{2}$ inch long, 5 mm. wide, .6 mm. thick at the middle; calyptra 10 mm. long \times 1.5 mm. thick; wall of capsule .03 mm. thick; spores .02 mm.; elaters .225 mm. long \times .01 wide.

Obs. The very large calyptra for this medium-sized plant is exceptional. In the whole of Stephani's 'Species Hepaticarum' he describes only a few with very large calyptra (5 mm. long); *A. longiflora* St. from Tasmania, 8 mm. long; *A. pulvinata* from Bolivia (Herzog), described as with "calyptra gigantea, 3 mm. long" [Printer's mistake probably!]; *A. maxima* (Schiffner) from Java and Sumatra, a plant 10 cent. long and 12 mm. wide having a calyptra 15 mm. long \times 2 mm. thick; my *A. macrantha* cannot be a small form of this, for it is monoicous with calyptra smooth.

Hab. Ignambi. On rocks by creek, 3000 ft. 1530.

ANEURA LOBATA (Schiffn.), St. in Bull. Herb. Boiss. vii. (1899) 761.

Riccardia lobata Schiffn. in Denkschr. Kais. Ak. Wien, lxvii. (1899) 178.

Hab. Mont Koghi. From bark and rocks, near stream, 1000 ft. Forest.

METZGERIA LUCENS St., Sp. Hep. Suppl. vi. (1917) 54.

Sterile; small; flaccid; ramose, branches postical; costa delicate, 3 to 4 cells thick, 2 antical and 2 postical cells, narrowly elliptic; antical plane, postical projecting; costa, wings, and margin without setæ; cells very large.

Dimensions. Stems 1 inch long, 1.5 mm. wide; costa .2 mm. wide; cells .15 mm. \times .125 mm.

Obs. Stephani records in Sp. Hep. Suppl. three species without setæ, two of which have very large cells, and one of them, *M. marginata* St., has very narrow (.036 mm. \times .09 mm.) marginal cells; he does not mention this character in his description of *M. lucens*, although he gives the size of the marginal cells of this species as .027 mm. \times .09 mm. Prof. Compton's plant agrees best with the brief description of *M. lucens*.

Endemic.

Hab. Ignambi. On gneiss rocks, in moist air, 3000 ft. 1531.

METZGERIA MARGINATA St., Sp. Hep. Suppl. vi. (1917) 55.

Dioicous; fronds 1 mm. wide; setæ on costa and margins only; cells .1 mm. \times .075 mm., marginal cells very small; only young ♀ seen.

Hab. Mont Arago. Bark of tree, in moist forest, 2000 ft. 1450.

HYMENOPHYTUM MALACCENSE St. in Hedwigia, xxxiv. (1895) 46; Sp. Hep. i. (1900) 307.

Obs. Marginal cells small; they, along with the 2 to 3 adjoining cells, firm; costa very broad, 5 cells thick and 15 cells broad, inner cells large, cortical cells small; 5 rows of double cells on each side of costa. Belongs to the *Podomitrium* section, as also does *H. Phyllanthus* (Hook.), from which it differs in being smaller, more rigid in texture, with much larger cells.

Hab. Igunambi. On gneiss rocks, in moist air, 3000 ft. 1531-1532.

HYMENOPHYTUM FURCATUM Pearson, sp. nov.

Dioica(?), mediocris vel elatiuscula pallide viridis cæspitosa. Caulis basin versus radiculosi; inferne exalati superne anguste alati furcati bifurcative, segmentis circa 10 latitudine æqualibus regularibus integris apice retusis, alis c. 20 cellulas latis, cellulis majusculis magnisve quadratis vel oblongo-quadratis leptodermibus, trigonis nullis; cellulis marginalibus similibus vel parvulis. Costa sectione transversâ oblongo-elliptica plano-convexa, antice convexa postice plana vel convexula, 8-12 cellulas crassa 15-20 cellulas lata, cellulis periphericis 50 et interiores simulantibus; costa fasciculis axialibus 1-2 fuscis e cellulis angustissimis compositis percursa.

Dimensions. Stems 1 to 1½ inch long; segments 1.25 mm., 1.5 mm., and 2 mm. wide; costa .3 mm. thick × .6 mm. broad, 2.25 mm. × .5 mm.; cells .075 mm. × .05 mm.

Obs. Belongs to the *Umbraculum* section; differs from *H. flabellatum* (Hook.) in its much larger size, segments one-half as many and not flabelliform; cells twice the size, usually elongate, with thin walls and no trigones; in *H. flabellatum* the walls are somewhat thick with distinct trigones.

Hab. Mont Canala. Covering rocks, near creek, 2500 ft., damp forest. 1211.

SYMPHYOGYNA NEOCALEDONICA Pearson, sp. nov.

Dioica, mediocris, pallide lutea, laxe cæspitosa. Caulis simplex vel ramos posticos parcos emittens; costa radiculosa, rhizoideis e cellulâ fuscâ emersâ ortis, sectione transversali anguste ovalis plano-convexa 6-8 cellulas crassa 10 cellulas lata; alæ irregulares hinc e latere uno absentes hinc parvæ lobatæ, sectione transversali costam versus 2-3 alibi 1 cellulas crassæ, 10-15 cellulas latæ (utraque ala); cellulæ magnæ quadratæ vel oblongo-quadratæ, cellulæ marginales majores quadratæ pachydermes. Squamæ crassæ lobato-laciniatæ, laciniis 20-25, 3 cellulas longis. Calyptra longa anguste cylindrica tenera hyalina 2 cellulas crassa, cellulis periphericis 40, ore plicato constricto ciliato, ciliis 20, 3 cellulas uniseriatis longis.

Dimensions. Fronds 1 inch long, 2 to 3 mm. wide; costa .5 to .7 mm. wide, 2 mm. thick; cells .06 mm × .07 mm., marginal cells .08 mm. × .08 mm.; involucre 1 mm. long × .75 mm. broad; calyptra 4 mm. × .4 mm., 3 mm. × .45 mm., .5 mm. × .4 mm.

Obs. The only other *Symphyogyna* recorded from New Caledonia is *S. picta* St., which has narrow marginal cells ($\cdot 027$ mm. \times $\cdot 07$ mm.) and a thick pyriform calyptra.

S. neocaledonica is distinguished by its large, thick, quadrate marginal cells, which give the plant a distinctly marginate appearance; the calyptra is also long, narrow, and very delicate.

Hab. Mont Koghi. On stones and earth, in spray of cascade, 1000 ft. 755.

TREUBIA INSIGNIS Goebel in Ann. Jard. Buit. ix. (1890) 1.

Hab. Mont Canala. Dense mats on old trunks, in damp forest, 2500 ft. 1207. Ignambi. Dead logs by creek, forest, 3000 ft. 1594.

Distrib. Java, Tahiti.

NOTOSCYPHUS PAROICUS Schiffn., Hepat. Buit. (1900) 83.

Hab. Mont Mou. On trees in high forest, 3500 ft. 616. Ignambi. On rocks by creek, 3000 ft. 1530. Ignambi. On gneiss rocks, in moist air, 3000 ft. 1532.

Distrib. Java, Sumatra, Banca, Ceylon, Nilgherries, Luzon, Tonkin.

HAPLOZIA COMPTONII Pearson, sp. nov.

Paroica, parva fusco-viridis laxe caespitosa. Caulis simplices radiculo-i rhizoideis purpureis. Folia patentia vel erecto-patentia amplexicaulia concava decurrentia dissita vel contigua oblonga integra, cellulis majusculis hexagonis plerumque longioribus quam latis, leptodermibus, trigonis nullis. Foliola nulla. Bractea foliis similes sed majores, basi saccatae sed antheridia nulla includentes. Perianthium e bracteis dimidio exstans fusiforme cylindricum loricatum 5-plicatum, carinis irregulariter crenulatis, ore parvo setuloso, setis c. 10.

Dimensions. Stems $\frac{1}{2}$ inch long, diam. $\cdot 3$ mm.; with leaves 1.5 mm. wide; leaves 1.25 mm. \times .9 mm., 1.1 mm. \times .8 mm.; cells $\cdot 04$ mm., $\cdot 06$ mm. \times $\cdot 04$ mm.; bracts 1.75 mm. \times 1.25 mm.; perianth 3 mm. \times $\cdot 75$ mm.

Obs. Only a few stems were met with, but with perianths; the saccate bracts indicate a paroicous inflorescence, but I was not able to meet with any antheridia; the narrow perianths bring it near to *Haplozia pumila* (Hook.), but they are more loricatae.

Hab. On rocks in stream, forest, 500 ft. 1958.

JAMESONIELLA BALANSÆ St. in Hedwigia, xxxiv. (1895) 46.

Stems 1 inch long; perianths terminal or with strong innovant postical branches with perianths, sometimes 4 on a stem; leaves subopposite; mouth of perianth ciliate.

Endemic.

Hab. Mont Mou. On trees in high forest, 3500 ft. 616.

PLAGIOCHILA COMPTONII Pearson, sp. nov.

Dioica, elata, fusco-viridis laxè cæspitosa. Caulès ramosi ramis divergentibus. Folia subopposita patentia (50°) vel erecto-patentia (30°) oblongo-ovata vel oblongo-triangularia, margine antico (inferiore) decurrente integro vel dentibus paucis distantibus armato, margine postico (superiore) curvato paulum ampliato ad caulis medium attingente, interdum ad basin reflexo, dentes magnos 7-15 gerente; apice truncato 2-3-dentato; cellulae pìrvulae vel mediocres, subrotundatae, pachydermes, trigonis nullis. Bractea late ovatae margine inferiore denticulato, superiore dentes magnos c. 15 gerente. Perianthium bracteis immersum parvum oblongo-quadratum complanatum, ore lato dentibus æquimagnis 35-40 ornato. Andræcia haud visa.

Dimensions. Stems 2 to 3 inches long; leaves 2.5 mm. \times 1.5 mm.; cells .03 mm.; bracts 2.5 mm. \times 1.5 mm.; perianth 2.25 mm. \times 1.5 mm.

Obs. I have compared this species with a great number from Asia-Oceania-tropica, but find none like it, the nearest being *P. Belangeriana* Lindenb., from which it differs in cell structure and in the small hidden perianth.

It has been referred by one authority to *P. nutans* St.; but I have had the opportunity of comparing it with the original, from which it is quite different.

Hab. Ignambi. Rising from rocks. Moist forest, 2000 ft. 1546.

PLAGIOCHILA LACINIATA Pearson, sp. nov.

Dioica, clatiuscula fusco-brunnea cæspitosa. Caulis parum ramosus, ramis ascendentibus. Folia subopposita vel alterna configua patenti-divergentia (70°) oblonga, margine antico (inferiore) recto vel parum curvato integro decurrente, margine postico (superiore) curvato ad caulis medium attingente, apicem versus paucidentato; apice truncato 2-4-dentato; cellulae mediocres subrotundatae pachydermes, trigonis nullis. Bractea oblongo-ovatae marginibus ambobus laciniatis, laciniis longis ligulatis simplicibus bifidisve perianthium circumvestientibus. Peranthium late breviterque obconicum ore laciniis longis fimbriato.

Dimensions. Stems 1½ to 2 inches long, diam. .2 mm.; with leaves 4 mm. wide; leaves 2 mm. \times 1 mm., 2.5 mm. \times 1 mm., 3 mm. \times 1.25 mm.; cells .035 mm.; bracts 2.75 mm. \times 1.5 mm.; perianth 1.5 mm. \times 1.5 mm., laciniæ 1 mm. to 1.5 mm. long; processes 3 mm. \times .3 mm., 1.5 mm. \times .2 mm.

Obs. Specimens of *P. fructicosa* Mitt. Bootang, Himalaya, coll. Rev. L. Dural, det. Schiffner (ex Herb. Levier) come nearest to it, but have a narrower leaf with fewer and coarser teeth, perianth with shorter and few laciniæ.

Why this species should be placed in section *Brevifolia* by Stephani I cannot understand.

Hab. Ignambi. Rising from rocks. Creek-side, moist forest, 2000 ft. 1546.

LOPHOCOLEA LEVIERI Schiffn. Hepat. Brit. (1900) 182.

Paroicus. Small, corticolous. Stems simple or slightly branched; leaves entire, rotuse, bidentate or pluridentate; underleaves free or slightly connate on one side, bifid to below the middle, with a small exterior tooth on each side; involucre and perianth relatively large; bracts dentate; bracteole dentate.

Dimensions. Stems $\frac{1}{4}$ to $\frac{1}{2}$ inch long, diam. .2 mm.; with leaves 1.5 mm. to 2 mm. wide; leaves 1.5 mm. \times .75 mm., 1 mm. \times .75 mm., .8 mm. \times .6 mm.; perianth 2.25 mm. \times 1 mm.

Obs. *Lophocolea Levieri*, named by Schiffner in honour of one of the most accurate and generous of Italian cryptogamic botanists, is recorded from Java and Sumatra; the New Caledonia specimens agree in every particular with Schiffner's description, except in being rather smaller.

Lophocolea Levieri is the only paroicus species belonging to this genus recorded from Asia and Oceania by Stephani, in his list of 267 species.

Our native *L. heterophylla* (Schr.) is described as monoicus, whereas it is usually paroicus. *L. Levieri* might well be regarded as the Eastern representative of *L. heterophylla*, as the range of variation in its leaves is from entire to paucidentate.

Hab. Mont Mou. On stones and mud in stream, 800 ft. 444. Mont Mou. On bark. 478. Mont Koghi. From bark and rocks, near stream, 1000 ft. Forest. 801. Mont Arago. On old fronds of a filmy fern. Moist forest, 1000 ft. No locality. 804.

Java, Sumatra.

CHILOSCYPHUS ARGUTUS Nees, Syn. Hep. 183; St., Sp. Hep. (1906) 215.

Leaves oblong-quadrate, apex rotundate, with 5-8 small teeth, marginal cells small; underleaves connate on both sides, bifid with 1 large marginal tooth at each side, sometimes 2. Androecia on short branches.

Hab. Mont Koghi. From bark and rocks, near stream, 1000 ft. Forest. 801.

Asia tropical and subtropical; Pacific Is. Australia and New Zealand subtropical.

CHILOSCYPHUS BEESLEYANA Pearson, sp. nov.

Dioica, mediocris olivaceo-brunnea caespitosa. Caulis simplex vel parum ramosus. Folia alterna imbricata horizontalia vel patenti-divergentia oblongo-quadrate vel ovato-quadrate, margine antico (inferiore) parum curvato decurrente, postico (superiore) curvato; apex quam basis triplo angustior truncatus late lunulato-retusus bidentatus segmentis divergentibus acutis; cellulae majusculae subrotundatae trigonis magnis. Foliola cum foliis ambobus anguste coalita, quam caulis 4-5-plo latiora, magna, ad medium vel altius bifida, sinu lato, segmentis acuminatis utroque lacinias 2 magnas curvatas extrorse gerente. Androecia ramis brevibus posticis disposita.

Dimensions. Stem 1 inch long; diam. of stem .2 mm.; with leaves 4 to 5 mm. wide; leaves 2 mm. long \times 1.4 mm. wide at base and .4 mm. at apex; 2.25 mm. \times 1.4 mm. at base and .4 mm. at apex, 2 mm. \times 1.25 mm. at base and .4 mm. at apex; cells .05 mm.; underleaves 1 mm. high \times 1.25 mm. broad; segments .75 mm.

Obs. I cannot refer this to any of the few (12) bidentate *Chiloscyphi*, recorded by Stephani from tropical Asia and Oceania.

I associate it with the name of my friend Mr. Hy. Beesley, who has given me a great number of Exotic Hepatics which have been very useful in the examination of the present collection.

Hab. Ignambi. On rocks by creek, 3000 ft. 1530.

CHILOSCYPHUS?

Obs. Fragments of a *Chiloscyphus* which I cannot refer to any described species, but too imperfect to name. Leaves opposite, quadrate or oblong-quadrate, apex shallowly bidentate, segments small, acute; underleaves narrowly connate with both leaves, quadrifid to the middle or below. Andrœcia small, catkin-like.

Hab. Mont Koghi. From bark and rocks, near stream, 1000 ft. Forest. 801.

CHILOSCYPHUS COMPTONII Pearson, sp. nov. (Pl. 2. figs. 6-19.)

Dioica, parva luteo-brunnea laxè caespitosa. Caulis simplex vel interdum ramum emittens, a fronte compressus, sectione transversâ 8 cellulas latus 6 cellulas altus, cellulis periphericis c. 20 interiores simulantibus, usque ad apicem radiculosus, rhizoideis pallide brunneis in fasciculos c. 10 filorum rectorum dispositis et e foliolorum basibus ortis. Flagella nulla. Folia subopposita horizontalia vel parum erecta patula imbricata recurvata irregulariformia oblongo-quadrata ovatave, apice truncato vel acuto vel bidenticulato; margine antico (inferiore) ad caulis medium attingente 3-5-dentato, ad angulum basalem decurrente acuto e caule fere latitudinis dimidio libero; margine postico (superiore) dentem magnum et auriculam rotundatam compressam, sectione transversâ angustè ellipticam, gerente. Textura flaccida; cellulæ majusculæ rotundatæ pachydermes, trigonis magnis; cuticulâ papillosâ. Foliola cum foliis utrinque cellularum ponte angusto coalita, quam caulis 4-5-plo latiora, c. 3-plo latiora quam alta, late subquadrata, margine superiore curvato 4-5-dentato, utrinque auriculâ compressâ rotundatâ coronata. Inflorescentia feminea postico-lateralis magna; bracteæ perianthii parti inferiori adnatæ in 3 paria dispositæ; paris infimi ovato-quadratæ, apice truncato, dentatæ, utriculæ subevolūtum gerentes; paris intermediati oblongo-quadratæ laciniato-dentatæ, ad $\frac{1}{4}$ plus minus bifidæ, sub-bracteolâ late ligulatâ dentatâ undulatâ; paris intimi teneræ admodum leptodermes ovatæ laciniatæ undulatæ, bracteolâ oblongo-quadratâ laciniato-dentatâ.

Perianthium inferne tubulare 4 cellulas crassum obovatum, bracteis immersum, trigonum alatum, alis irregularibus angustis vel latis (1-6 cellulas latis) margine crenulato; superne alis longis multis (9), perianthio adnatis, fere e basi ad apicem percurrentibus, irregularibus undulatis, interdum apice liberis linguiformibus, ornatum; os perianthii latum 3-lobatum, lobis quibusque lacinias c. 10 longas (6-10 cellulas longas) gerentibus. Calyptra tenera archegoniis 8 rubellis vel basin versus vel sparsim ornata. Capsula ovalis leptodermis pariete unistrato; pedicellus inferne sectione transversâ cellulas periphericas 18 quadratas (8 cell. in diametro), sectione longitudinali cellularum quadratarum pallide brunnearum ordines 35-40, exhibens. Sporæ numerosissimæ minutissimæ rotundatæ læves pallide rubello-brunneæ margine pallidiore distinctæ (tamen perfecte maturæ). Elateres pauci dispiri, spiris plus minus 15-plo circumvolutis.

Inflorescentia mas postico-lateralis seu vere postica; amenta brevina e bractearum 4-5 paribus dense imbricatarum composita secunda ovalia ventricosa, lobo bifido, segmentis acutis, lobulo paulum minore; antheridia spherica solitaria; bracteola ovato-acuta bidentata.

Dimensions. Stems $\frac{1}{2}$ to 1 inch long; diam. of stem .225 mm.; with leaves 2 mm. wide; leaves 1 mm. long \times .75 mm. wide; cells .04 mm.; underleaves .8 mm. wide \times .3 mm. high; lowest bracts 1.25 mm. \times .6 mm.; bracts 1.5 mm. \times 1 mm.; perianth 2 mm. \times 1.5 mm. upper portion; archegonia .225 mm. \times .05 mm.; pedicel 1 mm. \times .02 mm.; capsule .75 mm. \times .5 mm.; spores .015 mm.; elaters .1 mm. \times .015 mm.; male bracts, lobe .5 mm. \times .3 mm., lobule .4 mm. \times .3 mm.; male bracteole .3 mm. \times .2 mm.; antheridia .15 mm.

Obs. This is a very remarkable species, near to *C. cymbaliferus* (Hook. f. & Tayl.), Gottsche, Lindenb., & Nees, from which it differs in many characters. I am surprised that none of our authorities has raised this species to full generic rank, as it has several characters separating it from *Chiloscyphus*.

Hab. Mont Koghi. Dense mat on upper surface of fallen log. Forest, 3000 ft. 740.

ZOOFSIS RIGIDA Pearson, sp. nov.

Dioica, parva hyalina, inter hepaticas repens, flagella postica aphylla radiculosa ecostata, e cellulis elongatis composita, emittens; rhizoideis numerosis in filorum fere seniorum hyalinorum fasciculos congregatis. Caulis simplex, vel ramos posticos paucos interdum attenuatos emittens, plano-convexus vel biconvexus, paginâ anticâ planâ vel parum convexâ (sectione transversâ) 4 cellulas latâ, cellulis 2 interioribus late oblongo-quadratis, cellulis marginalibus pachydermibus (trigoni nullis), interne quadratis, externe conicis vel rotundatis liberis eminentibus, in paria approximatis (sinu angusto interjecto), et apicibus setas singulas minutas erectas vel hamatas striolatas gerentibus; paginâ posticâ convexâ (sectione transversâ) 4 cellulas

latâ, cellulis 2 interioribus minutissimis costam obtegentibus et 2 lateralibus (intramarginalibus) quadratis vel oblongo-quadratis.

Inflorescentia feminea ramulo postico brevi orta; bracteæ e cellulis teneris oblongis compositæ lanceolatæ acuminatæ. Perianthia et andrœcia laud visa.

Dimensions. Stems $\frac{1}{2}$ inch long, .5 mm. wide, .2 mm. thick; costa .05 mm. wide; middle antical cells 1.5 mm. \times 1 mm., marginal cells 1 mm.; setæ .075 mm. long; bracts .4 mm. long.

Obs. Differs from *Z. setulosa* Leitgeb in being more robust and rigid: in the marginal cells having a narrow sinus between two of them, not a large gap; setæ usually longer and narrower; perichæatial bracts small and very delicate, composed of narrow elongate delicate cells, quite different from the stem cells; in *Z. setulosa* the cells of the bracts are large, similar to the cells of the stem.

Hab. Ignambi. On gneiss rocks, in moist air, 3000 ft. 1531.

NOWELLIA BORNEENSIS (De Not.), Schiffner.

Dioicous. Minute, 3 to 4 cells wide, pale yellow in colour; creeping amongst other hepatics. Stem simple or with few postical branches, radiculose, rhizoids single, long, hyaline, with suckers. Leaves distant, alternate, often secund, semi-amplexicaul, erect, usually parallel with the stem, bifid to the middle or below, segments setaceous, 4 to 8 uniseriate cells long, 2 cells wide at the base, hamato-incurved or spreading, proceeding from the angles of the lobe, lobe 4 cells wide at the mouth, cucullate, inflated, keel smooth, arcuate; cells small, quadrate, walls thin, no trigones. No underleaves. Inflorescence ♀ on short postical branches; bracts broadly lanceolate, bifid to about the middle, segments acuminate, serrate. Andrœcia on short postical branches, 3 to 4 pairs of perigonial bracts, closely imbricate, oval, lobe acute, lobule similar, almost equal in size; antheridia oval.

Dimensions. Stems $\frac{1}{4}$ to $\frac{1}{2}$ inch long; diam. of stem .05 mm.; with leaves .3 mm. wide; leaves, lobe .15 mm. \times 1 mm., .15 mm. \times .15 mm., setæ .1 mm. to .2 mm. long; cells .02 mm.; perigonial bracts .2 mm. \times .125 mm.; antheridia .075 mm. \times .05 mm.

Obs. One of the smallest and most beautiful of hepatics; De Notaris's figures are fairly good and enable the species to be recognized.

Nowellia currifolia (Hook.) from Japan, of which I have seen specimens (Mt. Yokagura, Tosa; coll. Shutai Okamura), agrees in every particular with our native species.

Hab. Mont Koghi. On upper surface of fallen log. Forest, 3000 ft. 740.

NOWELLIA LANGII Pearson, sp. nov. (Pl. 2. figs. 20-34.)

Dioica, parva pallide brunnea dense cæspitosa. Caulis repentes radiculosi, rhizoideis plurimis hyalinis sæpe hapterophoris, simplices vel postice

pauci-ramosi, 5 cellulas lati, sectione transversâ cellulis periphericis 10, interioribus 5×5 . Folia secunda amplexicaulia ascendentia, lobo palmato late lanceolato laciniato-ciliato, lobulo rotundato lævi sed carinâ papillis 4 prominentibus prope lobum exornatâ; cellulis majusculis anguste oblongo-quadratis paulum pachydermibus, trigonis nullis. Foliola nulla.

Inflorescentia feminea ramulo postico brevi orta; bracteæ ovales acutæ serrulatæ fere ad medium bifidæ, segmentis lanceolatis acuminatis; bracteola bracteis similis. Perianthium ultra bracteas dimidio emersum lineare acute trigonum e cellularum elongatarum (sectione transversâ 120) strato unilamellato compositum, ore lato setis (2-3 cellulas longis, ad basin 2 cellulas latis) c. 50 ornato.

Andrœcia e ramis longis tenuibus orta; bracteæ in paria fere 10 dispositæ, quam folia minores inflatæ ovales, ad $\frac{1}{4}$ vel $\frac{1}{3}$ bifidæ, segmentis acutis, parum dentatæ.

Dimensions. Stems $\frac{1}{2}$ to 1 inch long; diam. of stem .1 mm.; with leaves .5 mm. wide; leaves, lobes with cilia .7 mm. long \times .6 mm. wide, lobule .15 mm. \times .15 mm.; cells .075 mm. \times .025 mm.; papillæ on keel .025 mm. \times .025 mm.; bracts 1.5 mm. \times .75 mm., segments .6 mm.; bracteole 1.75 mm. \times .6 mm.; perianth 3 mm. \times .5 mm.; setæ at mouth .1 mm.; perigonial bracts .3 mm. \times .2 mm., segments .1 mm.

Obs. Hitherto only three species belonging to this genus were known—our native *N. curvifolia* (Hook.), *N. borneensis* (De Not.) from Malaya, and *N. Wrightii* (G.) from Cuba.

The genus was named by Mitten after old John Nowell, a Lancashire working-man botanist; my friend the late Dr. Carrington had a great regard for him; his accurate knowledge of mosses and hepatics was only equalled by his generosity and kindly nature.

N. Wrightii (Gottsche) from Cuba, Dominica, and Guadeloupe is undoubtedly near to this species; it is, however, a smaller plant of a purple-rosy colour, with leaves less ciliate, with cells smaller and more quadrate, and devoid of the 3 to 4 large papillæ on the keel, although some of the keels are slightly papillose; bracts shorter and broader, less serrulate; perianth smaller and broader in proportion (1.75 mm. \times .5 mm.); mouth with fewer and more delicate setæ.

Hab. On rotting wood, Maxwells Hill, Perak, Malaya (Prof. W. H. Lang). Ignambi. On rocks by creek, 2000 ft. 1530.

MASTIGOBRYUM MARGINATUM St., Sp. Hep. (1908) 449.

Obs. The remarkable character of this hepatic is that the underleaves have a limbus of several cells deep, composed of thin-walled cells, quite different from the others; Stephani describes the margin of leaves as minutely crenulate, I should say "minutely denticulate-serrate on the upper margin, entire or almost so on the lower," leaves tridentate, under-

leaves reflexed, three times broader than the stem, much broader than high.

Endemic.

Hab. Mont Koghi. On upper surface of fallen log. Forest, 3000 ft. 740.

LEPIDOZIA CHÆTOCARPA Pearson, sp. nov. (Pl. 2. figs. 35-51.)

Dioica, parva corticola. Caulis fusco-rubello-brunneus, ramis et foliis pallide-brunneis, radiculosa; rhizoideis cinereo-albis in florum 4-8-norum (haptera magna gerentium) fasciculos congregatis, rhizoideis rameis haptera pauciora et minora gerentibus; flagella pauca aphylla radiculosa emittens; sectione transversâ cellulas 4 angustas latus, cellulis periphericis magnis 12, interioribus 8×8; regulariter pinnatus, ramis lateralibus dissitis alternis fere æquilongis. Folia horizontalia vel ascendentia oblique inserta, usque ad basin 3-secta (raro 2- vel 4-secta), cruribus subulatis rectis cellulas uniseriatis 10-12 longis; folia ramea biceruria quam caulina longiora, cuticulâ striolatâ. Foliola transverse inserta quam folia minora 3-4-cruria—caulina parva 3-4-cruria, cellulis longis, ramea longiora patentia.

Inflorescentia feminea e ramulo postico brevi orta; bracteæ ad $\frac{3}{4}$ laciniato-lobatæ, disco cellulas 2-4 alto, 8 lato; perianthium magnum oblongo-obconicum, e cellulis elongatis unistratis compositum, ciliis multis longis simplicibus vel biceruribus vestitum, ore lato longe ciliato.

Andrœcia intercalaria ramis posticis brevibus orta; bracteæ perigoniales in paria 4-5 dispositæ dense imbricatæ secundæ bicerures, disco cellulas 3-4 alto, 4-5 lato; antheridia solitaria ovalia.

Dimensions. Stems $\frac{3}{4}$ inch long, diam. 1 mm. to .125 mm.; with leaves 1.25 mm. wide: stem crura .7 mm. long; cells .1 mm. long × .02 mm. broad; underleaves .25 mm. high × .3 mm. wide; branch underleaves crura .7 mm. long; bracts 1.25 mm. high, disc .4 mm. high; bracteole 1.25 mm. long × .4 mm. wide, disc .4 mm. high; perianth 1.75 mm. × .75 mm., cilia at mouth .5 mm. to .75 mm.; perigonal bracts .3 mm. long, disc .1 mm. wide, segments .15 mm. long; antheridia .08 mm. × .06 mm.

Obs. This is a very remarkable species, the delicate perianth being clothed with numerous long cilia.

Hab. Mont Koghi. On upper surface of fallen log. Forest, 3000 ft. 740.

TRICHOCOLEA COMPTONII Pearson, sp. nov.

Sterilis; mediocris vel elatiuscula triste viridis dense cespitosa lanosa. Caulis flaccidus teres, diametro cellulas 15 lato, cellulis periphericis quam interioribus minoribus et fuscioribus, nudus bipinnatus, pinnis patentibus (50°) vel erecto-patentibus (30°) alternis; pinnulis alternis, utrinque 3-4 dispositis, sub-æquilongis. Folia paulo oblique inserta alterna, caulina patentia, ramea arcte imbricata, 6-lobata, disco brevi cellulas 2 alto 24 lato, lobis basi cellulas 4 latis irregulariter et longe pinnatis, cruribus et lateralibus

et anticis et posticis; cellulis majusculis oblongo-quadratis striolatis. Foliola 4-fida, disco cellulas 1-2 alto 12 lato, lobis basi cellulas 4 latis pinnatis, cruribus longis.

Dimensions. Stems 1 to 2 inches long, diam. .3 mm. to .4 mm.; with leaves 1.5 mm. wide; leaves, disc .1 mm. to .2 mm. high \times .4 mm. to .6 mm. broad, lobes .6 mm. long \times .2 mm. wide at base, crura .3 mm. to .4 mm. long; cells .06 mm. \times .04 mm.; underleaves, disc .2 mm. high.

Obs. Although this species agrees with Stephani's description of the disc (.2 mm. high \times .4 mm. broad) and 6-lobate leaf-form of *T. lerifolia*, the leaves are striolate, the plant not rigid but flaccid, and dull green in colour; the crura proceeding from all round the lobes give it a woolly appearance, which is noticeable in the dried specimens of the plant.

Hab. Mont Mou. On stones and mud, in stream. 800 ft. 442.

TRICHOCOLEA GENICULATA Pearson, sp. nov.

Dioica, mediocris vel elatiuscula pallide brunnea, ramis junioribus pallidioribus, dense caespitosa. Caulis a fronte compressus, sectione transversâ cellulas interiores 20×20 transverse paulo elongatas, cellulas periphericas parvas 50 exhibens, paraphyllosus, rigidus bipinnatus, pinnis alternis dissitis horizontalibus vel paulo ascendentibus, pinnulis in paria 5 dispositis, oppositis sensim decrescentibus. Folia geniculata erecta transverse vel paulo oblique inserta, caulina dissita arcte adpressa 4-lobata, lobis fimbriatis, disco cellulas 4-5 alto 20 lato, cruribus capillaceis oppositis omnino lateralibus brevibus (cellulas uniseriatis 7-10 longis) sub-æquilongis (apicali paulo longiore); cuticulâ dense striolatâ; cellulis majusculis quadratis vel oblongo-quadratis pachydermibus, trigonis nullis. Folia ramea arcte imbricata. Foliola transverse inserta 2-3-lobata, lobis ciliatis sub-æquilongis, disco cellulas 2 alto.

Planta mas tenerior; andrœcia e caule vel e ramis tenuibus orta; bracteae perigoniales in paria 4-5 dispositæ saccatæ, disco magno cellulas 4 alto; antheridia solitaria ovali-rotundata e stipite longo orta.

Dimensions. Stems 1 to 2 inches long, diam. .3 mm.; with leaves .5 mm. wide; crura of leaves .4 mm. long; cells of disc .04 mm., .05 mm., of crura .07 mm. \times .025 mm.; underleaves, disc .4 mm. high; perigonal bracts .7 mm. \times .35 mm.; antheridia .25 mm. \times .2 mm.

Obs. Distinct from any of the few *Trichocoleæ* recorded from Asia-Oceania. *T. breviseta* St. (New Guinea) and *T. striolata* St. (Luzon) have nude stems. The geniculate stem-leaves and the short subequal crura distinguish this species at once from any *Trichocoleæ* from Asia-Oceania.

Hab. Ignambi. On rocks by creek, 2500 ft. 1592. Ignambi. Rising from rocks. Creek-side, moist forest, 2000 ft. 1546.

BALANTIOPSIS NEOCALEDONICA Pearson, sp. nov. (Pl. 3. figs. 1-8.)

Sterilis; mediocris pallide viridi-brunnea caespitosa. Caulis simplex vel pauci-ramosus radiculosus, rhizoideis robustis purpureis. Folia contigua

alterna patenti-divergentia transverse inserta conduplicata oblongo-ovalia vel oblongo-quadrata, margine integro, interdum lobi margine superiore (postico) dentibus 1-2 magnis armato, apice 3-5-dentato, lobulo antico erecto quam lobo 4-plo minore oblongo-quadrato, usque ad medium et ultra 3-6-laciniato, segmentis lanceolatis; cellulæ mediocres oblongo-quadratæ leptodermes trigonis nullis, marginales longæ angustis-imæ; cuticula lævis. Foliola dissita cauli æquilata, usque ad medium et ultra bifida, segmentis divergentibus simplicibus vel furcatis lanceolatis acuminatis.

Dimensions. Stems 1 inch long, diam. .1 mm. to .15 mm.; with leaves 1.25 mm. wide; leaves, lobes 1 mm. \times .5 mm., lobule .4 mm. high \times .3 mm. broad; cells .04 mm. \times .03 mm., .05 mm. \times .03 mm.; marginal cells .075 mm. \times .015 mm.; underleaves .4 mm. \times 1.5 mm. broad at base.

Obs. This is the first species of the genus recorded from Asia-Oceania, the few other species being chiefly found in New Zealand and the Southern Hemisphere.

Balantiopsis angustifolia St. from Chili, of which I have seen specimens, has narrower leaves with different cell-structure, cells only half the size.

Balantiopsis diplophylla (Hook.) has larger antical lobules, lobes with more teeth, the upper (postical) margins toothed to the base, cells with large trigones, underleaves larger with laciniate segments.

Hab. Ignambi. On gneiss rocks, in moist air, 3000 ft. 1531.

RADULA LACERATA St., Sp. Hep. iv. (1910) 155.

Leaves irregularly laciniate, lobule narrowly rectangular, twice as long as broad, trigones large.

I have met with the male plant, which Stephani does not describe. Stems more delicate, leaves less lacerate, andrœcia on short branches, 4 to 5 perigonal bracts, smaller than the leaves, lobe acuminate, lobule almost equal in size, bracts swollen.

Endemic.

Hab. Mont Koghi. On upper surface of fallen log, forest, 3000 ft. 740.

RADULA FARMERI Pearson, sp. nov. (Pl. 3. figs. 9-19.)

Dioica (?), parva pallide olivacea stratificata. Caulis pinnatus ramis brevibus patenti-divergentibus vel patentibus. Folia arcute imbricata alterna patenti-divergentia semi-rotundata acuta apiculatave, lobi margine inferiore fere recto vel parum curvato, superiore curvato ampliato, caulem transeunte vel obtegente; lobulus quam lobus 3-4-plo minor subquadratus, ad caulis medium attingens, angulo libero obtuso, parum emarginato sinu acuto, superne complanatus inferne inflatus, carinâ arcuatâ, lævi; cellulæ parvulæ vel mediocres subrotundatæ pachydermes, trigonis nullis.

Inflorescentia feminea in caule vel in ramo terminalis innovationibus binis suffulta; bractearum lobus anguste ovalis integer acutus; lobulus quam lobi dimidium paulo major ovalis, apice rotundato emarginato interdum bis vel

ter inciso ; perianthium ultra bracteas parum emersum longe obconicum, ore lato fimbriato segmentis cellulas uniseriatis 5-15 longis.

Dimensions. Stems 1 inch long, diam. .2 mm. to .25 mm. ; with leaves 2.5 mm. wide ; leaves, lobe 1.25 mm. \times .85 mm., lobule .4 mm. \times .4 mm., lobe 1.1 mm. \times .9 mm., lobule .4 mm. \times .4 mm. ; cells .03 mm. ; bracts, lobe 2 mm. \times 1 mm., lobule 1.25 mm. \times .75 mm. ; perianth 2.25 mm. \times 1 mm. ; fimbriae at mouth .05 mm. to .1 mm. long.

Obs. There are only 13 species enumerated by Stephani belonging to the *Acutifolia* section of *Radula*, to which this belongs.

It is remarkable in having the free angle of the lobule emarginate ; only two such species are recorded by Stephani—*R. Delessertii* St. from the Mascarene Islands, which is described by Stephani as with apex of lobule slightly emarginate, and *R. sinuata* G. from Brazil with apex of lobule narrowly and deeply emarginate.

I have pleasure in associating with this unique species the name of Prof. Farmer, who has named several of the species in this collection. His breakdown in health prevented him from completing the work, which I much regret, although it has given me the opportunity of studying an exceedingly interesting set of plants.

Hab. Ignambi. On rocks by creek, 3000 ft. 1530.

RADULA VIELLARDII Gottsche ex St. in Hedwigia, xxiii. (1884) 150 ; St., Sp. Hep. iv. (1:10) 226.

Dioicous. Small, pale brown in colour, epiphytic. Stems irregularly branched. Leaves approximate, lobe horizontal (90°), oblong, antical (upper) margin covering the stem, lobule patent (50°), roundish-subquadrate, with apex obtuse, rarely acute, tumid at the base, extending to the middle of the stem, upper portion complanate ; texture delicate, cells medium size (.03 mm.—.04 mm.) ; cuticle slightly papillose. Bracts very large ; lobe oblong, erect. Perianth tubular, cylindrical, or narrowly clavate, slightly papillose, mouth entire.

Male plant more delicate, catkins numerous, 6 to 10 pairs of bracts, lobe spreading, apex obtuse, lobules closely imbricating.

Dimensions. Stems $\frac{1}{2}$ inch long, diam. .2 mm. ; with leaves 1.75 mm. wide ; leaves, lobe .8 mm. \times .65 mm., lobule .4 mm. \times .4 mm. ; cells .03 mm., .04 mm. ; perianth 3 mm. \times .8 mm.

Obs. The strikingly large bracts and the spreading lobes of the male bracts readily distinguish this species from others.

Stephani says (in Hedwigia, 1884, p. 150) that he has never seen the plant ; and there are several discrepancies between Gottsche's description in Hedwigia and his own 'Species Hepaticarum.'

Stephani says perianth clavate ; I find it to be equal in breadth the whole length or narrowly clavate : also he says leaves with large trigones ; I see none.

Endemic.

Hab. Mont Arago. On old fronds of a filmy fern. Moist forest, 1000 ft. 1447.

RADULA NIGRA Pearson, sp. nov.

Dioica (?), mediocris fusco-brunnea vel nigra laxe caespitosa. Caulis rigidus ligneus dichotomus. Folia imbricata concavula oblonga, lobo patenti-divergente (70°), margine antico (superiore) caulem obtegente; lobulus erecto-patens (30°) magnus, quam lobus 3-4-plo minor, rotundato-quadratus altior quam latus, caulem fere obtegens, angulo libero obtuso vel rotundato, inflatus, carinâ arcuatâ. Textura firmissima, cellulis quadratis 4-5-6-gonis, trigonis parvis.

Inflorescentia feminea immatura in caule; alioqui sterilis.

Obs. So far as I know, no other *Radula* like it has been described from New Caledonia or the Far East.

Dimensions. Stems 1 to $1\frac{1}{2}$ inch long, diam. .2 mm.; with leaves 2.25 mm. wide; leaves, lobes 1.25 mm. \times .9 mm., lobule .6 mm. high \times .4 mm. broad, .6 mm. \times .5 mm.; cells .025 mm.

Hab. Mont Koghi. From bark and rocks, near stream, 1000 ft. Forest. 801.

PLEUROZIA CALEDONICA (Gottsche), St., Sp. Hep. iv. (1910) 238.

Physotium caledonicum Gottsche ex Jack in Hedwigia, xxv. (1886) 81, tab. 8.

Obs. The segments of the leaves in Mr. Compton's specimens are longer and more acute; the leaves are also papillose; this is not mentioned in Jack's or Stephani's descriptions.

Endemic.

Hab. Mont Koghi. Drooping outwards in large masses from living trunks in scrubby forest, 3200 ft. 741.

FRULLANIA (Galeiloba) *BESCHERELLEI* St., Sp. Hep. iv. (1910) 456.

Dioicous. Medium size, dark brown in colour; corticolous. Stems pinnate or bipinnate; radiculose, rhizoids proceeding from base of underleaves, few, tufted, dark purple; branches often curved, sometimes attenuate. Leaves imbricate, concave, ovato-oblong to orbicular, apex rotundate, antical margin roundly appendiculate; lobule cucullate, erect or slightly divergent, stylus minute, 5 or 6 uniseriate cells long; cells smallish to medium, with irregular walls; trigones small and indistinct. Underleaves sub-rotund, often a little longer than broad, slightly decurrent, margin often reflex at the base and channelled in the middle, undulate, irregular, to one-third bifid, segments obtuse, connivent, sinus orbicular, margin reflexed. Androecia on short branches, oval; 6 pairs of bracts, closely imbricate; lobe oval, apex rotundate; lobule smaller, oval, apex obtuse.

Dimensions. Stems 1 to $1\frac{1}{2}$ inch long; diam. of stem .15 mm.; with leaves

1.25 mm. wide; leaves, lobes 1 mm. \times .9 mm., .6 mm. \times .475 mm., lobule .2 mm. high \times .175 mm. broad; cells .03 mm.; underleaves .25 mm. \times .25 mm.; perianth 1.25 mm. \times .75 mm.; andrœcia 1.5 mm. \times 1 mm.; perigonial bract, lobe .75 mm. \times .5 mm., lobule .6 mm. \times .3 mm.

Obs. I have had the opportunity of comparing my specimens with the original, named by Stephani, with which they agree in every respect.

At once distinguished from any other species by the remarkable orbicular sinus; the segments are connivent or nearly so, with their inner margins slightly reflexed. I have seen nothing like it anywhere else.

Var. *EXPLANATA* Pearson, var. nov. Lobulis explanatis; stylo minutissimo cellulas 4 uniseriatis longo.

Hab. Port Ngea. Creeping on tree-roots and rocks. *Acacia spirorbis* woods. 26. Woods near Port Despointes. On stones and bark on the ground. 175. Ermitage Stream. On trunk fallen across stream. 194.

Distrib. Tahiti.

FRULLANIA (Homotropantha) *COMPTONII* Pearson, sp. nov.

Dioica (?), clata, rubello-brunnea laxè cæspitosa. Caulis geniculatus irregulariter bipinnatus, pinnis longis, pinnulis brevibus curvatis. Folia horizontaliter inserta (90°) imbricata concava late ovata apiculata, margine inferiore (postico) recto vel curvulo, superiore (antico) curvato ad basin rotundato caulem transeunte vel amplius; lobulus minutus clavatus compressus dependens papillosus; stylus minutus cellulas uniseriatis 2-3 longus; cellulae parvulae nodulosæ, trigonis magnis. Foliola quam caulis 3-4-plo latiora approximata subrotundata, sæpe longiora quam lata, fere ad $\frac{1}{4}$ bidentata, segmentis acuminatis, sinu rotundato.

Inflorescentia feminea ramulis brevibus orta; bractearum lobus lanceolatus acuminatus laciniatus, lobulus quam lobus dimidio minor linearis laciniatus; bracteola oblongo-ovalis laciniata ad medium vel ultra bifida, segmentis lanceolatis.

Dimensions. Stems 2 to 3 inches long, diam. .2 mm.; with leaves 2 mm. wide; leaves, lobe 1.5 mm. \times 1 mm., 1 mm. \times .75 mm., lobule .2 mm. \times 1 mm., .15 mm. \times .075 mm.; cells .025 mm.; underleaves .75 mm. \times .75 mm., 6 mm. \times .6 mm., 6 mm. \times .5 mm. wide, segments .15 mm.; bracts, lobe 1.5 mm. \times .6 mm., lobule .1 mm. \times .2 mm.; bracteole .75 mm. \times .5 mm., segments .45 mm.

Obs. Differs from *F. papilliloba* St. from New Caledonia in having leaves usually apiculate, large trigones, very small lobule, segments of underleaves acuminate.

From *F. Kehdingiana* St. in having broadly ovate leaves, underleaves not five times broader than the stem, nor cordiform with broad acute segments.

From *F. pallidissima* St. in having a very small lobule, underleaves not cordiform and much smaller.

From *F. utriculata* St. in having very small lobule, underleaves not broadly reniform (twice as long), bracts laciniate, not entire.

Hab. No locality. 1730.

FRULLANIA (*Diastaloba*) **MICROSCOPICA** Pearson, sp. nov. (Pl. 3. figs. 20-34.)

Monoica, minuta, pallide rubello-brunnea, supra muscos et hepaticas repens. Caulis prostratus parce radiculosus irregulariter ramosus. Folia horizontaliter oblique inserta patula imbricata alterna semi-ovata vel ovata vel falcato-ovata, margine denticulato ciliato vel fimbriato, margine antico (superiore) curvato ampliato caulem transeunte, postico inferiore recto vel curvulo, apice obtuso vel acuto vel apiculato; lobus sæpe hyalinus; lobulus fusco-brunneus a caule dissitus obliquus comparate maximus lobo æquilongus clavatus; stylus comparate magnus triangularis apice obtuso vel acuto; cellulae minutissimæ quadratæ vel oblongo-quadratæ, trigonis nullis; cuticula tenuiter papillosa vel levis. Folia parva cauli æquilata oblonga, usque ad medium et ultra bifida; segmentis subulatis, sinu angusto.

Inflorescentia feminea sessilis vel e ramo brevi orta; bractearum lobus lanceolatus acuminatus minute crenulatus; lobulus quam lobus fere $\frac{1}{3}$ minor lineari-lanceolatus acuminatus; bracteola lineari-lanceolata, usque ad $\frac{1}{3}$ bifida, segmentis acuminatis, sinu angusto; perianthium pyriforme obovatum triquetrum, postice obtuse et late carinatum, antice planum, carinis levibus.

Andræcia intercalaria; bractea perigoniales in paria 4-5 dispositæ arcte imbricatæ; lobus ovatis acutus vel apiculatus, lobulo consimilis sed minor.

Dimensions. Stems $\frac{1}{4}$ inch long, diam. .05 mm.; with leaves .1 mm. wide; leaves, lobe .3 mm. \times 2 mm., .25 mm. \times .2 mm., .25 mm. \times .15 mm.; lobule .15 mm. \times .075 mm.; stylus .075 mm. \times .05 mm.; underleaves 1 mm. \times .05 mm.; cells .01 mm., .01 mm. \times .0125 mm.; bract, lobe .4 mm. \times .175 mm., lobule .3 mm. \times .075 mm.; perianth .55 \times .325 mm.; perigonal bract, lobe .225 mm. \times .15 mm., lobule .2 mm. \times .1 mm.

Obs. This is by far the smallest *Frullania* I have ever seen; and no species to my knowledge approaches it; the lobes of the leaves are often hyaline, while the lobules, which are relatively very large, are dark brown.

The plant is in perfect condition, with ♀ and ♂ abundant: so it is of its normal size and not a branch of a larger species.

Stephani notes after his description of *F. perversa* from the Philippine Is. (Sp. Hep. vol. iv. p. 639, 1911):—"This plant is one of the smallest known Hepatics, only *Microlejeunea* comes near it."

F. microscopica differs from it in many particulars.

Hab. Mont Mou. On trees in high forest, 3500 ft. 616.

ACROLEJEUNEA COMPTONII Pearson, sp. nov.

Dioica (?), mediocris fusco-rubello-brunnea corticola. Caulis irregulariter dichotomus firmus. Folia arcte imbricata patent-divergentia (70°) sub-

opposita concava, margine incurvato, semi-rotundata, margine antico (superiore) arcuato ad basin truncato caulem obtegente, postico (inferiore) recto vel parum curvato, apice rotundato interdum obtuso; lobulus quam lobus 4-plo minor oblongo-quadratus, 2-plo latior quam altus, margine libero recto integro, angulo acuto vel acuminato, superne complanatus, inferne inflatus, carinâ paulo arcuatâ, lævi; cellulæ parvulæ rhomboides parietibus irregularibus, trigonis parvis. Foliola imbricata, margine superiore inflexo, late breviterque cuneata decurrentia quam caulis 4-5-plo latiora, apice recto vel parum retuso, basin versus medio canaliculata.

Andrœcia in caulibus primariis intercalaria; bracteæ perigoniales quam folia paulo minores, inflatæ, lobo ovali rotundato, lobulo $\frac{1}{3}$ minore ovali obtuso.

Dimensions. Stems 1 inch long, diam. .2 mm.; with leaves 1.5 mm. wide; leaves, lobe 1 mm. \times .75 mm., lobule .5 mm. \times .25 mm.; cells .02 mm. \times .015 mm.; underleaves .5 mm. high \times .6 mm. broad; male bracts, lobe .75 mm. \times .5 mm., lobule .5 mm. \times .3 mm.; antheridia .15 mm. \times .1 mm.

Obs. Although no fertile stems have been met with, the other characters separate this plant from the other *Acrolejeunea* recorded by Stephani from Asia-Oceania. *Acrolejeunea cucullata* (Nees) would appear to be the nearest, but this has leaves broadly ovate, apex twice narrower than base, lobule with free angle obtuse or bi-angular, underleaves sub-rotund.

Hab. Mont Mou. On trees in high forest, 3500 ft. 616.

LOPHOLEJEUNEA MUENSIS St. in Hedwigia, xxxv. (1896) 110.

Var. *MICROLOBA* Pearson, var. nov.

Monoica. Caulis irregulariter pinnatus: folia late ovata, apicibus obtusis (folia ramea acuta), ad basin anticum truncato-rotundata, trigonis parvis; lobulus parvus quam lobus 6-7-plo minor, triangularis inflatus, angulo libero acuto; foliola quam caulis 3-plo latior. Inflorescentia feminea in ramo longo terminalis, innovationibus nullis; bracteæ oblongo-ellipticæ acutæ dentatæ; bracteola subrotundata integra. Andrœcia in ramis brevibus terminalibus.

Dimensions. Stems 1 inch long, diam. 0.1 mm.; with leaves 1.5 mm. wide; leaves .9 mm. \times .6 mm., lobe .9 mm. \times .6 mm., lobule .15 mm. \times .15 mm., underleaves .3 mm. \times .3 mm.

Obs. The few stems met with of this *Lopholejeunea* differ from Stephani's description of *L. muensis* from New Caledonia in the smaller size of leaves .9 mm. \times .6 not 1.5 mm. \times 1.17 mm., the much smaller lobules 6 to 7 times smaller than the lobes, not 3 times smaller, underleaves 3 times broader than stem, not 5 times; but as it agrees in its inflorescence, its olive colour, irregular pinnate stems, leaves broadly ovate, antical base truncato-rotundate, branch leaves acute, bracts oblongo-elliptic, acute, margin near apex irregularly dentate, it is probable that Mr. Compton's specimens are only a variety

of it; if further specimens distinguish it, I propose the name of *LOPHOLEJEUNEA MICROLOBA* for it.

Endemic.

Hab. Mont Koghi, from bark and rocks, near stream, 1000 ft. Forest. 801.

BRACHIOLEJEUNEA MACROBRACTEOLA Pearson, sp. nov.

Dioica (?), *mediocris pallide brunnea corticola prostrata*. Caulis irregulariter pauci-ramosus. Folia horizontalia (90°) vel patenti-divergentia (70°) arcute imbricata sub-opposita concava semi-rotundata, margine antico (superiore) arcuato caulem obtegente, postico (inferiore) fere recto vel paulo curvato; lobulus quam lobus fere 4-plo minor ovalis superne complanatus inferne inflatus, margine minute mamillato, mamillis 3-6 unicellulatis, carinâ arcuatâ lævi; cellulæ mediocres oblongo-quadratæ, cellulæ marginales minores quadratæ. Foliola approximata quam caulis 3-4-plo latiora, sub-reniformia vel orbicularia, cellulis marginalibus minoribus.

Inflorescentia feminea terminalis innovationibus binis suffulta; bractearum lobus ovalis, apice obtuso; lobulus similis fere æquimagnus; bracteola maxima ultra perianthium emersus late cuneata. Perianthium inter bracteas immersum oblongo-ovatum 10-plicatum, carinis obtusis lævibus.

Andrœcia haud visa.

Dimensions. Stems 1 inch long; diam. of stem .15 mm.; with leaves 1.5 mm. wide; leaves, lobe 1 mm. \times .5 mm., .9 mm. \times .6 mm., .75 mm. \times .6 mm., lobule .4 mm. \times .25 mm.; cells .03 mm.; underleaves .4 mm. high \times .6 mm. broad, .4 mm. \times .5 mm.; bracts, lobe 1 mm. \times .5 mm., lobule .9 mm. \times .5 mm.; bracteole 1.3 mm. \times 1.3 mm.; sub-bracteole 1.2 mm. \times 1.2 mm.; perianth 1.5 mm. \times .75 mm.

Obs. No *Brachiolejeunea* recorded from Asia-Oceania approaches this species.

Hab. *Casuarina*, near ground, very dry conditions. 91. Mont Koghi. On upper surface of fallen log. Forest, 3000 ft. 740. Ermitage Stream. On trunk, fallen across stream. 194. Mont Arago. On old fronds of a filmy fern. Moist forest, 1000 ft. 1447.

DREPANOLEJEUNEA COMPTONII Pearson, sp. nov.

Dioica (?), *minuta hyalina supra muscos hepaticasque repens*. Caulis simplex vel furcatus, ramis paucis cellulas 3 latis, radiculosus, rhizoideis paucis hyalinis. Folia erecta (10°) vel erecto-patentia (30°) alterna dissita; lobus ovalis vel ellipticus acutus vel ovali-acuminatus, apice reflexo, margine superiore (antico) ad caulis medium vel paullo ultra, inferiore (postico) ad caulis medium, attingente; lobulus paulo minor ovalis inflatus, carinâ paulo arcuatâ lævi; cellulæ minutæ quadratæ vel oblongo-quadratæ leptodermes, trigonis nullis. Caulis appendiculis (an foliis imperfectis?) numerosis parvis triangularibus instructus. Foliola bicurva, cruribus divergentibus cellulas 4 uniseriatis longis, disco humili cellulas 2 alto.

Dimensions. Stem $\frac{1}{4}$ inch long, diam. .04 mm. to .05 mm.; with leaves .225 mm. wide; leaves, lobe .2 mm. \times .1 mm., .25 mm. \times .1 mm., .15 mm. \times .1 mm., lobule .15 mm. \times .075 mm., .125 mm. \times .075 mm.; cells .02 mm. \times .02 mm., .03 mm. \times .015 mm.; underleaves, setæ .075 mm. long.

Obs. In the list of *Drepanolejeunea* from Asia and Oceania-tropica, in Stephani's 'Species Hepaticarum' there is none to which this minute species can be assigned; it is the smallest member of this genus that I have met with.

Hab. Mont Koghi. On upper surface of fallen log. Forest, 3000 ft. 740.

DREPANOLEJEUNEA MICROCARPA Pearson, sp. nov.

Dioica, minuta pallide- vel fusco-brunnea foliicola radiculosa, rhizoideis cinereo-albis. Folia patenti-divergentia (70°) vel erecto-patentia (30°) alterna dissita vel contigua, sæpe unilaterialia, contorta semi-ovata subrectangularia acuta vel acuminata uncinata dentata; folia ramea sæpe integra; lobulus magnus, quam lobus dimidio minor vel jam vero exiguior, inflatus involutus, carinâ arcuatâ lævi vel paullo papillosâ; cellulae parvulae quadratae 4-5-6-gonæ, trigonis parvis sed evidentibus, ocellis paucis parvis, cuticulâ lævi vel minute papillosâ. Foliola minuta ad medium et ultra bifida, segmentis divergentibus cellulas 4 uniseriatis longis, disco cellulas 2 alto \times 4 lato.

Inflorescentia feminea ramo brevi terminalis innovatione singulâ suffulta; bractearum lobus late lanceolatus acutus vel acuminatus denticulatus, lobulus 2-3-plo minor lanceolatus vel linearis integer vel paullo denticulatus; bracteola ovalis ad $\frac{1}{4}$ vel $\frac{1}{3}$ bifida, segmentis acuminatis inconspicue denticulatis, sinu acuto; perianthium parvum pyriforme 5-carinatum, carinis lævibus, rostellatum.

Androecia intercalaria vel e ramis brevibus orta; bractea perigoniales arete imbricatae, lobus rotundatus vel minute acutus, lobulus paullo minor, carinâ papillosâ vel lævi.

Dimensions. Stems $\frac{1}{4}$ inch long, diam. .05 mm.; with leaves .4 mm., .5 mm. wide; leaves, lobe .3 mm. \times .2 mm., lobule .15 mm. \times .1 mm.; cells .025 mm.; underleaves .1 mm. \times .05 mm.; bracts, lobe .45 mm. \times .2 mm., .45 mm. \times .175 mm., lobule .35 mm. \times .1 mm., .3 mm. \times .05 mm.; perianth .4 mm. \times .3 mm.; perigonal bracts .2 mm. \times .175 mm.

Obs. Its nearest ally is *D. dactylophora* (Nees), from which it differs in its dentate leaves, not spinose; small but distinct trigones; bracts and bracteole denticulate, not spinose; and the minute perianth .4 mm. \times .3 mm., not .83 mm. \times .59 mm., with keels smooth, not spinose.

D. uncinata St. is autoicous, leaves lanceolate, perianth obovate, .83 mm. \times .58 mm.

Hab. Mont Mou. On trees in high forest, 3500 ft. 616. Mont Koghi. Upper surface of fallen log. Forest, 3000 ft. 740.

LEPTOLEJEUNEA VITREA (Nees), St., Sp. Hep. v. (1913) 389.

Jungermannia vitrea Nees, Enum. Hep. Javan. 56.

Lejeunea vitrea Nees, Syn. Hep. 402.

Dioicous. Minute, hyaline or pale grey in colour, creeping on other hepatics. Stem irregularly branched, 2 to 3 cells wide. Leaves, lobe erectopatent (30°), approximate, oval-acute, upper portion serrate, antical (upper) margin extending to the middle of stem, base narrow, lobule patent-divergent (70°), 4 times smaller than the lobe, oval, twice as long as high, involute, free angle acute, tumid, keel arcuate, smooth; cells smallish to medium size, 4-5-6-sided quadrate, ocelli irregularly disposed or linear, 3 to 6 large. Underleaves 3 times broader than the stem, broadly quadrate, 2 cells high by 3 broad, with 4- to 6-celled uniseriate crura proceeding from the middle or upper angle, sometimes 1 or 2 minute teeth below the crura.

Inflorescence ♀ on short branches; bracts, lobe lanceolate-acuminate, entire, or with 1 or 2 teeth, lobule similar but smaller; bracteole lanceolate-acute, bifid to below the middle, entire. Perianth obovate, cornute, horns long, obtuse, margin entire.

Male plant more delicate, catkins long. 4 to 6 pairs of bracts, closely imbricate

Dimensions. Stems $\frac{1}{2}$ inch long, diam. .075 mm.; with leaves 1 mm. wide; leaves, lobe .9 mm. \times .4 mm., lobule .35 mm. \times .2 mm.; cells .03 mm., ocelli .04 mm. \times .035 mm.; underleaves .4 mm. \times .1 mm.; bracts, lobe .5 mm. \times .15 mm., lobule .4 mm. \times .1 mm.; bracteole .3 mm. \times .15 mm., segments .15 mm.; perianth .6 mm. \times .4 mm.

Obs. I have had the opportunity of comparing my specimens with those under this name collected by Balansa in New Caledonia and determined by Stephani; they entirely agree with them.

Hab. Ermitage Stream. Epiphyllous on Fern and *Freyinetia*, etc. 145. Java, New Guinea, Philippine Islands.

LEPTOLEJEUNEA DOLABRIFORMIS Pearson, sp. nov.

Dioica, parva brunnea vel albescens supra folia repens. Caulis irregulariter bipinnatus cellulas 2 latus. Folia contigua patula alterna parum concava vel plana suboblungo-quadrata, margine inferiore (postico) recto vel parum curvato, superiore (antico) recto vel ad basin versus curvato et caulem aliquantum obtegente, apice truncato vel parum hamato et acuto, margine integro; cellulæ parvulæ quadratæ pachydermes, trigonis nullis, ocellis lineariformibus 3-6-cellularibus vel irreglariter dispositis; lobulus ovatus paullo longior quam altus involutus, angulo libero acuto, quam lobus 4-5-plo minor, interdum nullus. Foliola late et breviter cuneata bisecta cruribus valde divergentibus horizontalibus vel paullo ascendentibus cellulas 5 uniseriatis longis.

Inflorescentia feminea ramo brevi posita vel sessilis. Bractæ parvæ, margine integro; lobus anguste oblongus; lobulus similis sed minor. Bracteola ovato-lanceolata, ad $\frac{1}{3}$ plus minus bifida, segmentis et sinu acutis, integra. Perianthium oblongo-triangular apice lato, 5-angulatum, angulis superne late alatis, alis triangularibus acutis, cornubus nullis.

Andrœcia sessilia vel in ramis brevibus posita, sphærica; bractæ in paria 3 dispositæ ovales, apice rotundato.

Dimensions. Stem $\frac{1}{4}$ to $\frac{1}{2}$ inch long, diam. .05 mm.; with leaves .8 mm. wide; leaves, lobe .5 mm. \times .3 mm., lobule .15 mm. \times .1 mm.; cells .025 mm., ocelli .06 mm. \times .035 mm.; underleaves .35 mm. wide, with setæ .075 mm. high; bracts, lobe .325 mm. \times .1 mm., lobule .25 mm. \times .05 mm.; bracteole .3 mm. \times .1 mm., segments .15 mm. \times .05 mm. at base; perianth .5 mm. \times .3 mm. wide at apex; amentula .3 mm. \times .3 mm.; bracts, lobe .2 mm. \times .15 mm., lobule .15 mm. \times .1 mm.

Obs. *Leptolejeunea rhombifolia* St. from New Caledonia has leaves with acute apex, entire or paucidentate, 1.25 mm. \times .58 mm., lobule large, 3 times smaller than lobe; perianth pyriform, .9 mm. \times .58 mm.; bracts, lobe, and lobule irregularly dentate.

Hab. Ermitage Stream. Epiphyllous on Fern, *Freycinetia*, etc. 145.

EULEJEUNEA PTERIDIS Bescherelle & Spruce in Bull. Soc. Bot. Fr. xxxvi. (1889) p. clxxxvii.

Lejeunea pteridis (Besch. et Spruce), St., Sp. Hep. v. (1915) 787.

Monoicous. Small; pale green in colour, creeping amongst other hepatics and mosses. Stem slightly branched. Leaves oblong, subfalcate, apex rotundate, narrow at base of insertion; lobule minute or wanting, oblong, free angle toothed. Underleaves oval to subrotund, bifid to below the middle, segments acute, sinus wide, obtuse. Bracts small, half size of perianth, entire, lobe oval, apex obtuse, lobule similar but smaller; bracteole oval, bifid to below the middle, segments obtuse, sinus acute. Perianth obovate to cuneate-pyriform, beak long. Andrœcia with 4 to 5 pairs of bracts, keel of bracts papillose.

Dimensions. Stems $\frac{1}{2}$ inch long, diam. .075 mm.; with leaves .1 mm. wide; leaves, lobe .6 mm. \times .4 mm., lobule .1 mm. \times .1 mm.; lobe .5 mm. \times .4 mm., lobule .1 mm. \times .075 mm.; underleaves .15 mm. \times .1 mm.; bract, lobe .4 mm. \times .2 mm.; bracteole .25 mm. \times .175 mm.; perianth .5 mm. \times .325 mm.

Obs. I have had the opportunity of comparing this with original specimens named by Dr. Spruce, from New Caledonia, collected by Balansa; and it agrees well with it.

Endemic.

Hab. Mont Koghi. On upper surface of fallen log. Forest, 3000 ft. 740. Mont Mo. On bark. 478.

EULEJEUNEA DENUDATA Pearson, sp. nov.

Sterilis. Mediocris pallide viridis laxè cæspitosa. Caulis firmus, cellulas 2-3 latus, remote et longe bipinnatus radiculosus, rhizoideis usque ad apicem dispositis, fasciculatis, divergentibus. Folia dissita vel contigua alterna patenti-divergentia (70°) semi-ovata vel semi-rotundata vel falcato-ovata integra, margine antico (inferiore) brevissime decurrente vel recto, postico (superiore) arcuato, ad caulis medium attingente, basi angustâ, apice rotundato; textura firma; cellulae mediocres quadratæ vel oblongo-quadratæ 4-5-6-gonæ, trigonis nullis, quædam majores, folia tamen haud conspicue ocellata; lobulus plerumque nullus, in ramis quibusdam tamen minutus ovalis tumidus. Foliola parva, cauli arcuè adpressa, quam caulis paulo latiora, ovalia vel subrotundata, ad $\frac{1}{2}$ bifida, sinu acuto vel rotundato, segmentis triangularibus acutatis, sæpe nullis.

Andrœcia in ramis brevibus posita. Bracteæ in paria 4 dispositæ; lobus rotundatus, lobulus similis sed minor.

Dimensions. Stems $\frac{1}{2}$ to $1\frac{1}{2}$ inch long; diam. of stem .1 mm.; with leaves 1.25 mm. wide; leaves, lobe .65 mm. \times .475 mm., .6 mm. \times .5 mm., lobule .15 mm. broad \times .1 mm. high; cells .03 mm., .01 mm. \times .03 mm., .04 mm.; underleaves .15 mm. high \times .1 mm. broad; perigonia} bracts .175 mm. \times .175 mm.

Obs. This is a remarkable *Lejeunea*; the distantly branched stems, texture of the stem and leaves, the absence of lobules on the larger forms give it somewhat the appearance of a *Calypogeia*, to which genus it had been referred by one authority.

It does not agree with the description of *L. aloba* St., Sp. Hep. v. (1915) 767, from New Caledonia, which name had already been appropriated by Sande Lacoste, Hep. Jav. 1856, 72, Tab. 13, and from which it is very different, according to the description and figures.

Hab. Mont Koghi. From bark and rocks near stream. Forest. 801. Igumbi. Attached to stones under water in running creek. Forest, 2000 ft.

MICROLEJEUNEA BRUNNEA Pearson, sp. nov.

Dioica, minuta rubello-brunnea, supra muscos et hepaticas repens, radiculosa, rhizoideis paucis hyalinis. Caulis simplex vel parèe ramosa, cellulas 3 latus, rigidus. Folia erecta, cauli parallela, alterna dissita vel contigua; lobus ovalis vel rotundatus, apice rotundato, margine antico (superiore) ad caulis medium attingente; lobulus plus minus $\frac{2}{3}$ minor, apice uni-dentato, dente sæpe incurvato, parte liberâ paulo involutâ, carinâ rotundatâ papillosâ; cellulae minutæ quadratæ, parietibus firmis, trigonis nullis. Foliola parva, quam caulis paulo latiora, orbicularia, ad medium plus minus bifida, segmentis obtusis. Bractearum lobus obovatus, apice rotundato; lobulus $\frac{1}{3}$ minor lanceolatus; bracteola obovata, ad $\frac{1}{3}$ bifida, segmentis acutatis.

Dimensions. Stems $\frac{1}{4}$ inch long; diam. of stem .04 mm.; with leaves .2 mm. to .25 mm. wide; leaves, lobe .2 mm. \times .15 mm., lobule .15 mm. \times

·125 mm.; cells ·015 mm., keel cells ·02 mm.; underleaves ·05 mm. \times ·05 mm.; bracts, lobe ·2 mm. \times ·125 mm., lobule ·125 mm. \times ·05 mm.; bracteole ·2 mm. \times ·125 mm., segments ·075 mm.

Obs. The constant reddish-brown colour distinguishes it at once from all other *Microlejeunea* I have seen.

Differs from *M. albicans* (Nees) in its colour and other characters given by Stephani, but agrees with the description of this species given by Evans in his Hawaiian Hepaticæ (Trans. Conn. Sc. vol. x. p. 445, 1900), except in the colour.

Hab. Mont Mou. On trees in high forest, 3500 ft. 616. Mont Koghi. On upper surface of fallen log. Forest, 3000 ft. 740. Ignambi. On rocks, by creek, 3000 ft. 1530.

LEPTOCOLEA COMPTONII Pearson, sp. nov. (Pl. 3. figs. 35-46.)

Monoica, parva pallidissime viridis vel alba, supra muscos et hepaticas repens. Caulis cellulas 3 angustas latus pinnatus, ramis brevibus. Folia imbricata; lobus patenti-divergens (70°) ovalis semi-oblongus vel obovatus, margine antico (superiore) arcuato caulem obtegente, postico (inferiore) recto vel curvato, apice rotundato; lobulus quam lobus 4-plo minor ovalis vel ellipticus, 2-plo latior quam altus, tumidus, margine superiore involuto, angulo libero obtuso, carinâ arcuatâ lævi. Textura tenerrima; cellulae mediocres quadratæ vel oblongæ 4-5-6-gonæ leptodermes, trigonis minutissimis. Foliorum margo integer e cellulis angustis hyalinis, quæ per instrumentum microscopicum oculis percipi vix possunt, compositus.

Flores femineæ crebræ, in ramis brevibus terminalibus positæ, vel innovatione singulâ florigerâ suffultæ; bractearum lobus ellipticus integer, ad instar foliorum hyalino-marginatus, apice obtuso; lobulus fere $\frac{1}{2}$ minor late lanceolatus, apice obtuso. Perianthium late pyriforme compressum, apice obcordato, antice planum, postice obtuse carinatum, marginibus integris.

Andræcia in ramis brevibus sita; bractere in paria 4 dispositæ; lobus ovalis, apice rotundato; lobulus similis sed minor.

Dimensions. Stems $\frac{1}{4}$ inch long, diam. ·06 mm.; with leaves 1·25 mm. wide; leaves, lobe 1 mm. \times ·7 mm., ·9 mm. \times ·6 mm., ·7 mm. \times ·55 mm., ·7 mm. \times ·45 mm., lobule ·3 mm. \times ·175 mm., ·3 mm. \times ·15 mm.; cells ·03 mm. \times ·05 mm., ·03 mm. \times ·04 mm., hyaline fringe cells ·03 mm. long, \times ·01 mm. wide; bract, lobe ·65 mm. \times ·3 mm., lobule ·4 mm. \times ·175 mm.; perigonal bract, lobe ·3 mm. \times ·2 mm., lobule ·2 mm. \times ·15 mm.

Obs. There is no *Leptocolea* listed by Stephani from Asia-Oceania near this; the beautiful hyaline fringe of narrow cells on the leaves is a striking character.

Leptocolea caledonica (Gottsche) has falcato-elliptic leaves (1·33 mm. \times ·3 mm.), lobule bidentate, bracts lanceolate or narrowly lingulate (1 mm. \times ·9 mm.), and no mention is made of any hyaline fringe of the leaves by Gottsche or Stephani.

Leptocolea cordiflora St., also from New Caledonia, has denticulate leaves.

Leptocolea limbata St., from the Philippine Is., is a much larger plant, fuscous brown, leaves ovate-elliptic, with large trigones, lobule apiculate, perianth obconical.

Hab. Ermitage Stream. Epiphyllous on Fern, *Freyinetia*, etc. 145.

LEPTOCOLEA CRENULATA Pearson, sp. nov.

Dioica (?), minuta hyalina foliicola. Caulis cellulas 2-3 angustas latus parce ramosus radiculosus, rhizoideorum fasciculo ad lobuli cujusque basin orto. Folia patula horizontalia (90°) vel patent-divergentia (70°) approximata ovalia semi-ovalia subfalcata, ad basin anguste inserta, apice rotundato obtuso (folia ramea acuta), margine antico (superiore) arcuato, ad caulis medium attingente, minute denticulato, postico (inferiore) recto vel paulum curvato minute crenulato; lobulus quam lobus fere 4-plo minor, ovalis incurvatus tumidus, angulo libero acuto, carinâ arcuatâ lævi; cellulae parvulae quadratae, basales majores elongatae leptodermes, trigonis nullis; foliorum quorundam cuticula minute papillosa.

Inflorescentia feminea in ramo brevi sita, innovatione singulâ suffulta: bractea quam folia minores lanceolatae acutae minute denticulae; lobulus quam lobus $\frac{1}{2}$ minor linearis acutus. Perianthium obconicum compressum, antice planum vel superne obscure carinulatum, postice obtuse carinatum, raro ad apicem versum acutulum; carinae superne paulo alatae: margo minute denticulatus.

Androecia haud visa.

Dimensions. Stem $\frac{1}{4}$ inch long, diam. .05 mm.: with leaves 1 mm. wide; leaves, lobe .6 mm. \times .4 mm., .6 mm. \times .325 mm., lobule .25 mm. \times .175 mm.; branch-leaves, lobe .45 mm. \times .25 mm., lobule .2 mm. \times .1 mm.; cells .025 mm.; bracts, lobe .4 mm. \times .2 mm., lobule .3 mm. \times .075 mm.; perianth .6 mm. \times .4 mm.

Obs. There are no species of *Leptocolea* recorded from Asia-Oceania-tropica with which this agrees. *L. cordiflora* St., also from New Caledonia, is the nearest, but differs in several characters.

Hab. Mont Arago. On old fronds of a filmy fern. Moist forest, 1000 ft. 1447.

COLURA SUPERBA (Mont.), St., Sp. Hep. v. (1916) 941.

Lejeunea superba Mont. in Ann. Sc. Nat. 3me Sér. x. (1848) 115.

Leaves remotely dentate, papillose; few stems only met with, without trace of inflorescence; these agree exactly with those in the Manchester Museum from New Caledonia under this name, determined by Dr. Spruce.

Hab. Ermitage Stream. Epiphyllous on Fern and *Freyinetia*, etc. 145? 1492.

Tahiti.

MEGACEROS CALEDONICUS St., Sp. Hep. v. (1916) 951.

Monoicous; walls of capsule without stomata; involucre with upper portion rugulose; spores .03 mm.; elaters abundant; androecia very numerous and aggregate.

Hab. Ermitage Stream. On stones in stream bed. 152. Mont Mou. On stones and mud by stream. 479. Mont Canala. On vertical clay stream banks, 900 ft., in open country. 1241. Ignambi. Rocks by creek, 3000 ft. 1593.

MEGACEROS MONOSPIRUS St., Sp. Hep. v. (1916) 953.

Monoicous; smaller than *M. caledonicus* St.; involucre smooth, 7 mm. long; capsule 25 mm. long, walls without stomata; spores .027 mm.; elaters monospirous; androecia few.

Hab. Tonine. Encrusting rocks in stream. Forest, 500 ft. 1958. Mont Canala. On rocks in stream. High forest, 900 ft. 1139.

ASPIROMITUS PARISII St., Sp. Hep. v. (1916) 968.

Monoicous; small size; involucre short, smooth; capsule stomatiferous; elaters numerous; androecia few.

Hab. Paompai. On clay soil. Forest margin, 1000 ft. 1883.

ANTHOCEROS LERATHI St., Sp. Hep. v. (1916) 989.

Monoicous; ♂ near to the ♀. Fronds 6 cells thick at the middle; cortical cells smaller and darker; capsule wall stomatophorous; no elaters.

Hab. Mont Mou. On stones and mud in stream, 800 ft. 444.

DENDROCEROS JAVANICUS Nees, Syn. Hep. (1844) 582; St., Sp. Hep. v. (1917) 1010.

Anthoceros javanicus Nees, Enum. Hep. Jav. pl. 1, n. 1.

Dendroceros granulatus Mitt. in Seem. Fl. Viti. (1865) 419.

Costa two to three times broader than thick; involucre tuberculate; capsule papulose; spores black, minutely asperous; elaters pale yellowish brown, with single broad ribbon.

Dimensions. Fronds $\frac{1}{2}$ to 1 inch long; cells .04 mm.; involucre 1 centim. long; capsule .5 mm. long; spores .04 mm.; elaters .2 mm. long \times .01 mm. broad.

Hab. Ignambi. Bark of fallen tree. Forest, 2500 ft. 1687.

Asia and Oceania-tropica.

DENDROCEROS CALEDONICUS St., Sp. Hep. v. (1917) 1012.

Hab. Mont Mou. On dead twigs in forest; rare. 617.

EXPLANATION OF THE PLATES.

PLATE 2.

Aneura pulcra Pearson, sp. nov.

- Fig. 1. Frond, half nat. size.
 2. The same, $\times 5$.
 3. Cross-section of stem, $\times 25$.
 4. Cross-section of pinna, $\times 25$.
 5. Bract, $\times 25$.

Chiloscyphus Comptonii Pearson, sp. nov.

- Fig. 6. Plants, ♂ and ♀, half nat. size.
 7. Portion of stem, antical view, $\times 12$.
 8. The same, postical view, $\times 12$.
 9, 10. Leaves, $\times 12$.
 11. Cross-section of utricle, $\times 25$.
 12. Portion of leaf, $\times 145$.
 13. Underleaf, $\times 25$.
 14, 15. Bracts, $\times 12$.
 16. Bracteole, $\times 12$.
 17. Perianth, explanate, $\times 12$.
 18. Male bract and bracteole, $\times 12$.
 19. Antheridium, $\times 25$.

Novellia Langii Pearson, sp. nov.

- Fig. 20. Plant, half nat. size.
 21, 24. Leaves, $\times 25$.
 25. Portion of leaf, $\times 115$.
 26. Papille on keel, $\times 145$.
 27, 28. Bracts, $\times 12$.
 29. Bracteole, $\times 12$.
 30. Perianth, $\times 8$.
 31. Cross-section of perianth, $\times 12$.
 32. Setæ at mouth of perianth, $\times 25$.
 33, 34. Perigonial bracts, $\times 25$.

Lepidozia chaetocarpa Pearson, sp. nov.

- Fig. 35. Plant, half nat. size.
 36. Stem, $\times 5$.
 36-38. Leaves, $\times 25$.
 39, 40. Branch-leaves, $\times 25$.
 41. Portion of one of the crura, $\times 145$.
 42. Underleaf of stem, $\times 25$.
 42a. Underleaf of branch, $\times 25$.
 43. Portion of bract, $\times 12$.
 44. Bracteole, $\times 12$.
 45. Perianth, $\times 12$.
 46-47. Portions of perianth with cilia, $\times 25$.
 48, 49, 50. Perigonial bracts, $\times 25$.
 51. Antheridium, $\times 25$.

PLATE 3.

Balantiopsis neocaledonica Pearson, sp. nov.

- Fig. 1. Plants, half nat. size.
2. Portion of young stem, antical view, $\times 25$.
3. The same, postical view, $\times 25$.
4. Leaf, $\times 25$.
5. Portion of leaf, $\times 145$.
6. Marginal cells, $\times 145$.
7, 8. Underleaves, $\times 25$.

Radula Farmeri Pearson, sp. nov.

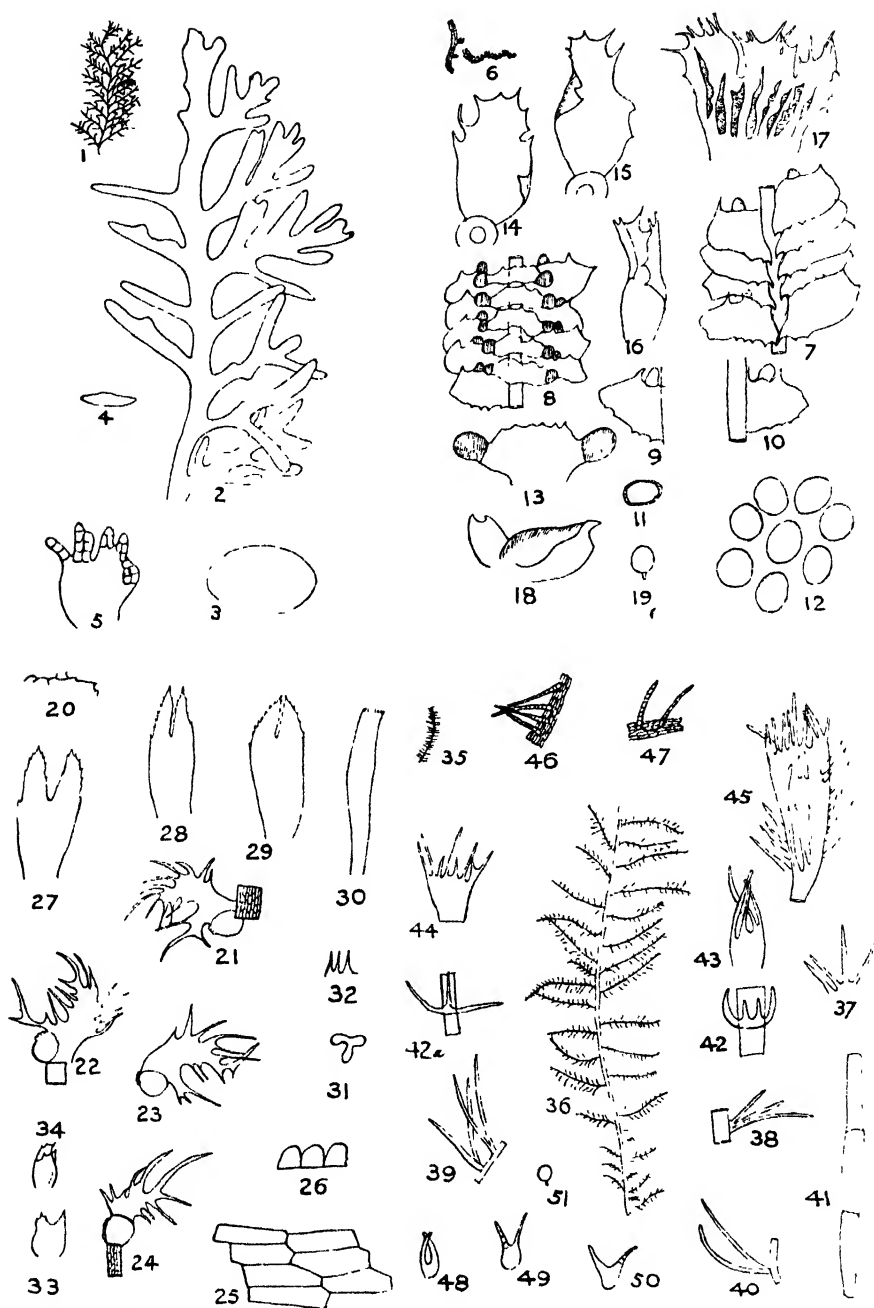
- Fig. 9. Plant, half nat. size.
10. Portion of stem, antical view, $\times 8$.
11. The same, postical view, $\times 8$.
12-14. Leaves, $\times 12$.
15. Free angle of lobule, $\times 25$.
16. Portion of leaf, $\times 145$.
17. Bract, $\times 8$.
18. Perianth, $\times 8$.
19. Portion of mouth of perianth, $\times 60$.

Frullania microscopica Pearson, sp. nov.

- Fig. 20. Plant, half nat. size.
21. Portion of stem, antical view, $\times 25$.
22. Portion of stem, postical view, $\times 25$.
23-31. Leaves, lobes, $\times 25$.
32, 33. Lobules with styli, $\times 25$.
34. The same, with underleaf, $\times 25$.
35, 36. Underleaves, $\times 25$.
37. Portion of leaf, $\times 145$.
38. Bract, $\times 25$.
39. Bracteole, $\times 25$.
40. Perianth, $\times 25$.
41. Androecia, $\times 25$.
42. Perigonal bract, $\times 25$.

Leptocolea Comptonii Pearson, sp. nov.

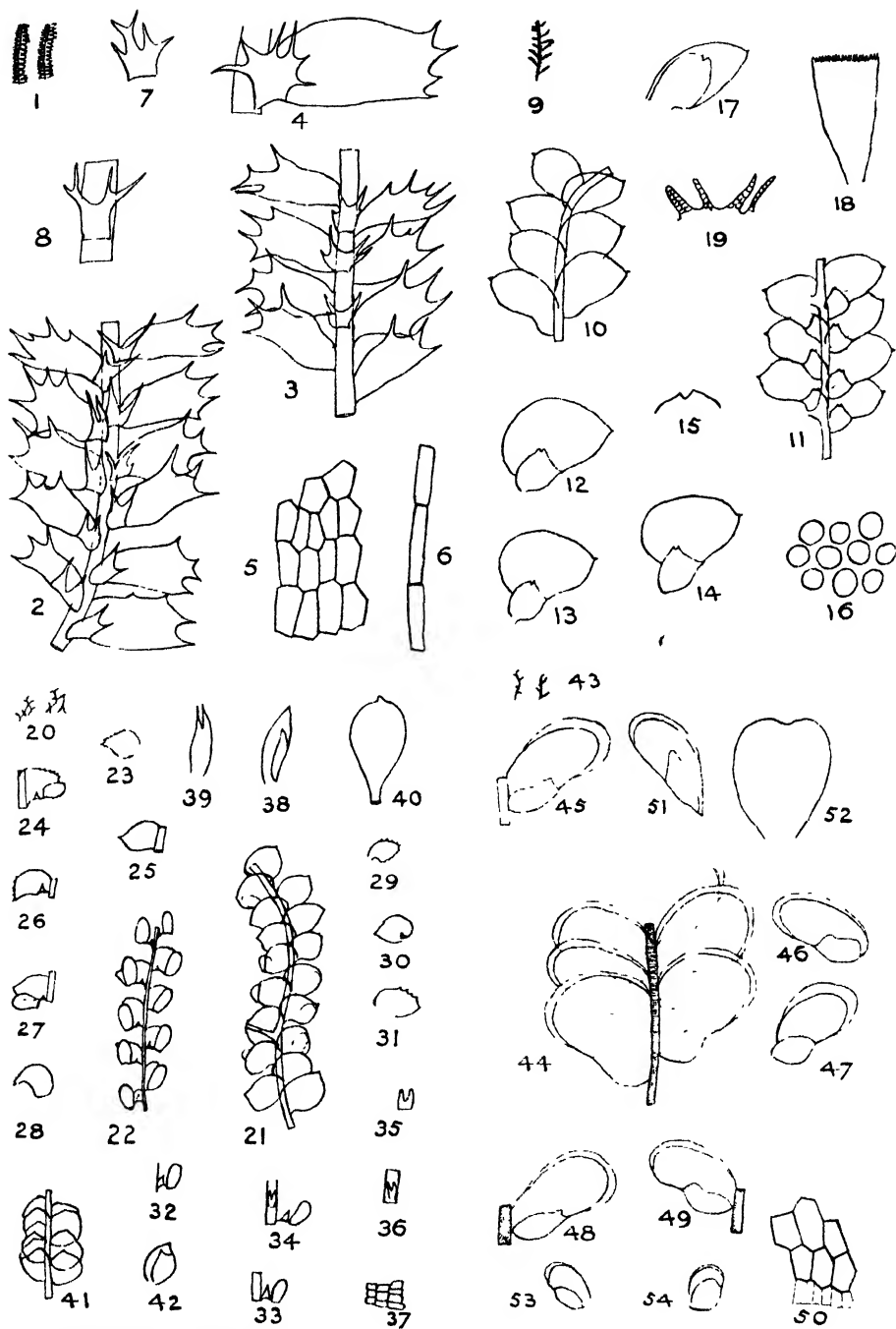
- Fig. 43. Plant, nat. size.
44. Portion of stem, postical view, $\times 25$.
45-49. Leaves, $\times 25$.
50. Portion of leaf, showing margin, $\times 145$.
51. Bract, $\times 25$.
52. Perianth, $\times 25$.
53, 54. Perigonal bracts, $\times 25$.



M. DIXON & W. H. PEARSON del.

GROUT sc

NEW CALEDONIAN HEPATICÆ.



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NEW CALEDONIAN HEPATICÆ.

MARINE ALGÆ.

By A. GEPP, M.A., F.L.S.

CHLOROPHYCEÆ.*ENTEROMORPHA COMPRESSA* Grev. Baie Ouémo ; on angiosperms. 112.*CHÆTOMORPHA NATALENSIS* Hering. Baie Ouémo ; on rocks at low-tide mark. 114.*DICTYOSPLERIA FAVULOSA* Decaisne. Baie Ouémo ; on rocks at low-water mark. 109.*POLYPHYSA PENICULUS* Ag. Baie Ouémo ; on rocks at low-water mark. 110.*HALIMEDA OPUNTIA* Lamour. Baie Ouémo ; at low spring-tide mark. 722.*HALIMEDA TUNA* Lamour. Baie Ouémo ; at low spring-tide mark. 723.*CODIUM SPONGIOSUM* Harv. Baie Ouémo ; washed up. 120.**PHÆOPHYCEÆ.***TURBINARIA ORNATA* J. Ag. Baie Ouémo ; washed up. 103.*CYSTOPHYLLUM MURICATUM* J. Ag. Baie Ouémo ; washed up. 124.*DICTYOTA FURCELLATA* Ag. Baie Ouémo ; washed up. 127.*SPHACELARIA FURCIGERA* Kuetz. Baie Ouémo ; epiphytic. 106.*SPHACELARIA TRIBULOIDES* Menegh. Epiphytic on floating *Turbinaria*. 122 (in part).**RHODOPHYCEÆ.***GRACILARIA CONFERVOIDES* Grev. Baie Ouémo ; on stones just below low-tide mark. 119.*CHAMPIA COMPRESSA* Harv. Epiphytic on stems of *Turbinaria*. 123.*ACANTHOPHORA ORIENTALIS* J. Ag. Baie Ouémo ; on stones just below low-tide mark. 117.

CHONDRIA DASYPHYLLA Ag. Baie Ouémo ; on stones below low-tide mark. 118.

LEVEILLEA JUNGERMANNIODES Harv. Baie Ouémo ; epiphytic on floating *Turbinaria*. 122 (in part).

CERAMIVM CLAVULATUM Ag. Baie Onémo, on shell &c. just below low-tide mark. 111.

FRESHWATER ALGÆ.

By NELLIE CARTER, D.Sc.

(PLATE 4.)

Introduction.

THE following is a list of freshwater algæ observed in collections made by Mr. R. H. Compton in New Caledonia in 1914. The algal flora of this island has not previously been investigated, although a certain amount of work has been done on some of the neighbouring islands. A consideration of the following works is important in dealing with the algal flora of New Caledonia :—

- BORGE, O.—Australische Süßwasser Chlorophyceen. Bihang till K. Sv. Vet.-Akad. Handl. xxii. No. 9, 1896.
- BORGE, O.—Über tropische und subtropische Süßwasser Chlorophyceen. Ibid. xxiv. No. 12, 1899.
- GUTWINSKI, R.—De Algis a M. Raciborski anno 1899 in Insula Java collectis. Bull. Akad. des Sciences Cracovie, 1902.
- MASKELL, W. M.—Contributions towards a list of New Zealand Desmidiæ. Trans. N. Zeal. Inst. xiii. 1881.
- MASKELL, W. M.—On the New Zealand Desmidiæ. Additions to Catalogue and Notes on Various Species. Ibid. xv. 1883.
- MASKELL, W. M.—Further Notes on the Desmidiæ of New Zealand. Ibid. xxi. 1889.
- MOBIUS, M.—Australische Süßwasseralgen. Flora, 1892.
- NORDSTEDT, O.—De Algis aquæ dulcis et de Characeis ex insulis Sandvicensibus a Sv. Berggren 1875 raportatis. Lund, 1878.
- NORDSTEDT, O.—Freshwater Algæ collected by Dr. S. Berggren in New Zealand and Australia. Kongl. Sv. Vet.-Akad. Handl. xxii. 1888.
- SCHMIDLE, W.—Einige Algen aus Sumatra. Hedwigia, xxxiv. 1895.
- SCHMIDLE, W.—Süßwasseralgen in "Die Flora der Samoa-Inseln." Engler's Botan. Jahrbuch, xx iii. 1896.

The collections proved to be very rich in diatoms, and the Cyanophyceæ also were very interesting, yielding one new genus, and two other species new to science. The filamentous Chlorophyceæ were fairly abundant, but unfortunately they were mostly in a sterile condition, and so could not be specifically determined. Desmids were not numerous, the genera *Closterium* and *Cosmarium* being best represented. On the whole the collections were made either from running streams or from subaërial habitats. This explains the relative abundance of diatoms and filamentous Chlorophyceæ on the one hand, and of Cyanophyceæ and other subaërial algæ on the other, and the comparative scarcity of such algæ as Desmids which require still water and permanent boggy conditions.

A number of ubiquitous species were present in the collections, but some of the species observed have hitherto only been recorded from one or other

of the neighbouring islands. For example, the interesting primitive lichen described by Schmidle from the Samoa Islands as *Scytonema Hieronymi* occurred in well-developed masses on tree-trunks in New Caledonia. Another lichenised alga, *Trentepohlia diulepta*, originally described from New Guinea, also occurs in New Caledonia. The discovery of *Closterium compactum*, described by Nordstedt from New Zealand, was also of interest. Further, the investigation has added considerably to our knowledge of the distribution of various algæ, since many species only hitherto known from localities very remote from New Caledonia occurred in the collections.

A list of localities is given below :—

132. *Baie Ouémo*. Irregular gelatinous masses on sandy soil; pale bluish-green when wet, black and shrivelled when dry. Abundant in coastal woods and in the open.
151. *Ermitage Stream*. Bright green spongy masses and small brackets projecting from twigs and branches over stream.
176. *Ermitage Stream*. Large bluish-green masses attached to stones a few inches below the surface in stream pools. Serpentine rocks.
193. *Ermitage Stream*. Subaerial; orange-yellow filaments in pendent tufts on dead trunks over stream; uncommon.
338. *Plaine des Lacs*. Mixture of gatherings from shallow rain pools, free floating and attached to leaves. Serpentine; 800 ft.
384. *Rivière du Carénage*. Algæ attached to rocks and plankton squeezed out. Serpentine; 800 ft.
528. *Mont Mou*. Green filamentous on rocks in stream. Cretaceous; 800 ft.
532. *Mont Mou*. Subaerial, brown filamentous, forming mat over trees. Damp gully forest; 600 ft.
612. *Mont Mou*. Bright orange-red incrusting rocks in slight shelter. Serpentine; scrub area; 2500 ft.
757. *Mont Koghi*. Orange filamentous, forming covering to serpentine rocks in a stream-course.
808. } *Riv. Dumbéa*. Squeezings of submerged algæ in rock pools of river. Serpentine;
809. } 200 ft.
810. *Riv. Dumbéa*. Red mud from small clear pool along stream. Serpentine; 200 ft.
811. *Riv. Dumbéa*. Soft incrustation of mud and algæ on dripping rocks by stream. Serpentine; 250 ft.
851. *Mont Dore*. Bright yellowish-green filamentous, mucilaginous; and squeezings. From pool in littoral zone, at mouth of small stream.
852. *Mont Dore*. Dull sage-green, mucilaginous, sparse growth; and squeezings. Pool in littoral, at mouth of small stream.
864. *Pic la*. Stiff gelatinous nodules, incrusting rock in a trickle of water. Brownish-green. Serpentine; 500 ft.
865. *Pic la*. Dense mat of dark green filaments on a nearly vertical surface of wet serpentine soil by stream. 500 ft.
879. *Baie Kuakué*. Bluish-grey, woolly coating in rock crevices; dry serpentine scrub; 1000 ft.

- 1045 *a, b, & c.* *Mont Humboldt.* Small creek; serpentine; 350 ft.
 1045 *a.* Soft, brownish, filamentous, not markedly gelatinous, attached to stones in rock pool.
 1045 *b.* Dense brown, rather gelatinous mats attached to roots or wet rocks.
 1045 *c.* Nodular incrustation on wet rocks; dark slaty colour.
 1181. *Mont Canala.* Large, rounded, black, ill-smelling mat on tree-trunk in moist forest; 1500 ft.
 1242. *Mont Canala.* Bright green filamentous attached to roots of *Jussiaea* and other plants in sluggish stream. Mica-schist clay; 900 ft.
 1356. }
 1357. } *Canala.* Mica-schist alluvium at sea-level.
 1358. }
 1359. }
 1356. Filamentous, dark green, on dead shoots of *Potamogeton* sp. in fairly swift stream.
 1357. Squeezings of *Lemna* sp. in stagnant pool, covered with duckweed and dead leaves.
 1358. Dead leaves with algæ attached, from same pool as 1357.
 1359. Squeezings of *Azolla* sp., from slowly running water in roadside ditch.
 1427. *Mont Arago.* Small, transparent, brownish-green blobs on rocks with hepatics by stream. Forest region; mica-schist; 1000 ft.
 1487. *Prompai.* Water from small rock pool in course of creek. Surface covered with golden-brown film. Shales; 300 ft.
 1986. *Ouendjam Forest.* Squeezings from *Potamogeton* leaves and stems in slowly running stream. Hornblende; 500 ft.
 2411. *Riv. Ngoye.* Light green mucilaginous filamentous growth covering bottom of large stagnant rock pool; probably with unicellular organisms. River-bed. Serpentine: 400 ft.

SYSTEMATIC.

FLAGELLATA.

DINOBYRON SERTULARIA Ehrenb. Plaine des Lacs. 338.

DINOFLAGELLATA.

Species of *Glenodinium* (Ehrenb.) Stein and *Peridinium* Ehrenb. occurred in No. 809, but since in every instance only the ruptured case left by the escaped swimmers remained, it was not possible to identify them. One was, however, probably *Glenodinium uliginosum* Schill.

CYANOPHYCEÆ.

CHROOCOCCACEÆ.

CHROOCOCCUS TURGIDUS (Kütz.) Näg. River Dumbéa; in rock pools.
 809. Europe, India, Malaya, America.

CHR. SCHIZODERMATICUS West. River Dumbéa ; incrusting dripping rocks near river. 811. Europe, Africa, America.

CHR. MINUTUS (Kütz.) Näg. River Dumbéa ; in washings of filamentous algæ in rock pools. 808, 809. Europe, Asia, Africa.

CHR. COHÆRENS (Bréb.) Näg. River Dumbéa ; in gelatinous incrustation on dripping rocks near river. 811. Europe, India, America.

SYNECHOCOCCUS CRASSUS Arch. Plaine des Lacs ; amongst other algæ in shallow rain pools. 338. Europe.

S. PARVULUS Näg. Mont Humboldt ; forming a film on the outside of a colony of *Ricularia* sp. 1045 a. Europe.

GLÆOCAPSA MAGMA Kütz. No locality. 89. Also another specimen with neither number nor locality. Europe, India, S. Africa.

G. MONTANA Kütz. Specimen of unknown locality. 1092. Europe.

G. POLYDERMATICA Kütz. River Dumbéa ; in gelatinous incrustation on dripping rocks near river. 811. Mont Humboldt ; in similar habitat. 1045 c. Europe, America.

G. MURALIS Kütz. River Dumbéa ; on dripping rocks near river. 811. Europe, W. Indies.

G. GRANOSA (Berk.) Kütz. River Dumbéa ; on dripping rocks near river. 811. Mont Humboldt ; on dripping rocks. 1045 c. Europe, America.

G. ÆRUGINOSA (Carm.) Kütz. Mont Humboldt ; on dripping rocks. 1045 c. Europe, Java.

GLÆOTHECE CONFLUENS Näg. River Dumbéa ; in gelatinous incrustation on dripping rocks. 811. Europe, Africa, America.

G. PALEA (Kütz.) Forti. River Dumbéa ; in gelatinous incrustation on dripping rocks. 811. Europe.

G. RUPESTRIS (Lyngb.) Born. River Dumbéa ; in gelatinous incrustation on dripping rocks. 811. Mont Humboldt ; in nodular incrustation on wet rocks. 1045 c. Europe, America.

G. VIBRIO, sp. nov. (Pl. 4. fig. 1.) Cellulis minimis, cylindraceis, curvulis, diametro 2-5 plo longioribus, singulis vel binis vel interdum ad 32 in familias ovaes consociatis, contentu pallide cœruleo, tegumento hyalino homogœneo. Long. cell. 2-5 μ ; crass. cell. 1-1.5 μ ; long. fam. 10-26 μ ; crass. 6-16 μ .

Canala ; subaerial, forming a thin mucous film with *Mastigocolæus obtusa*,

sp. nov., and *Rosaria ramosa*, sp. et gen. nov., on trees. 1181. River Dumbéa ; amongst other Cyanophyceæ in gelatinous coating on wet rocks near stream. 811. Nearest to *G. violacea* Rabenh., from which it differs in the greater diameter of the cells, and the formation of larger colonies, with unstratified sheaths.

OSCILLATORIA(Æ).

OSCILLATORIA VIOLACEA (Wallr.) Hass. Canala ; in washings of *Azolla* from roadside ditch. 1359. Europe, America.

LYNGBYA DISTINCTA Schmidle. Mont Canala ; epiphytic on various aquatic objects. 1242. Sandwich Islands.

SYMPLOCASTRUM CUSPIDATUM Forti (*Symplocacuspidatum* W. & G. S. West). Forming *Symploca*-like tufts over Bryophytes. 587. England, W. Indies.

NOSTOC(II)ACEÆ.

NOSTOC COMMUNE Vauch. Baie Ouémo ; on sandy soil. 132. Ubiquitous.

N. SPHÆRICUM Vauch. Mont Arago ; with Hepatics on rocks near stream. 1427. Europe, Australia, America.

?N. MACROSPORUM Menegh. Forming a thin incrustation on rocks. (Probably this species, but identification uncertain because the alga had been dried for a long time and could not be satisfactorily restored.) No number nor locality.

SCYTONEMA(Æ).

SCYTONEMA SUBTILE Möb. Baie Kuakué ; forming bluish-grey woolly coating in rock crevices. 879. The alga only differed from the one described by Möbius in that it occurred as a definite stratum, not as isolated filaments amongst other algæ. India, Australia.

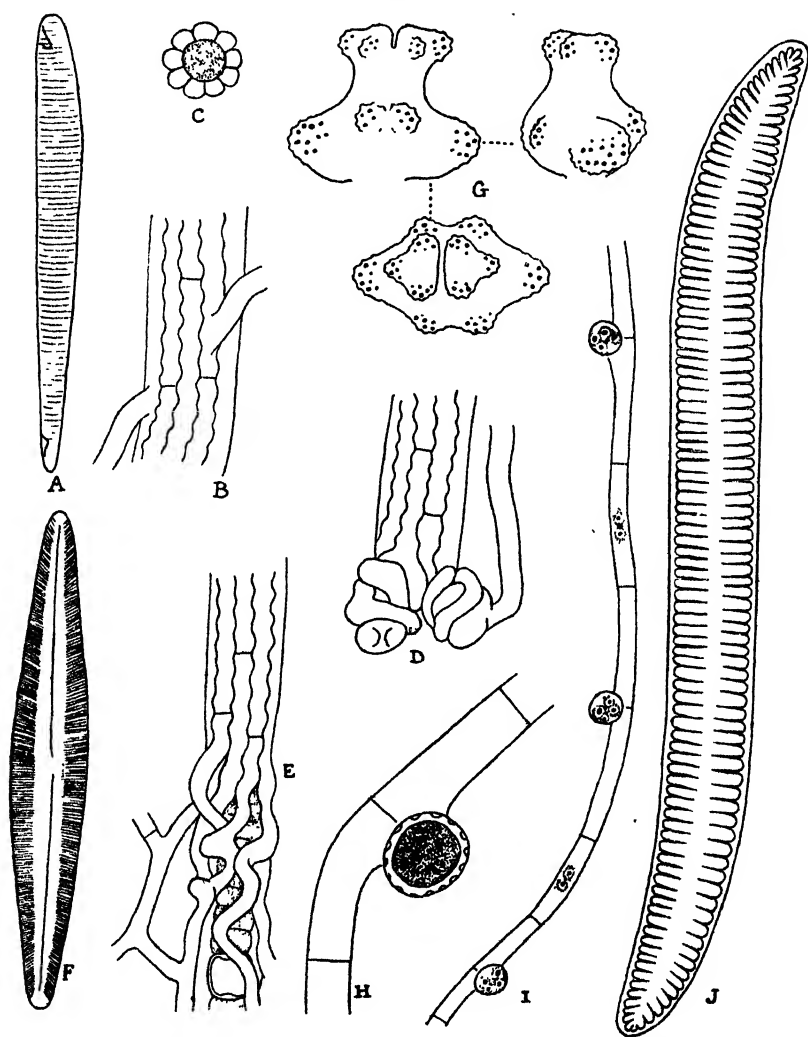
S. AMPLUM W. & G. S. West. Forma trichomatibus gracilioribus. Crass. fil. 16–22 μ ; crass. trich. 1.5–2 μ ; long. cell. 20–29 μ ; Mont Humboldt ; on wet rocks and in rock pools. 1045 a, 1045 b, 1045 c. River Dumbéa ; in small clear pool. 810. Pic Ia ; forming a mat on nearly vertical surface of wet serpentine soil near stream. 865. W. Indies.

S. VARIUM Kütz. With *Cephaleuros virescens* on leaf. 563. Only a very little present. Europe, Ceylon, Malaya, America.

S. HIERONYMI Schmidle, Flora Samoa-Inseln, 1896, p. 254. (Text-fig. 1, B–E.) With mosses on tree-trunks. 1087. Samoa Islands. This alga, first described by Schmidle from the Samoa Islands, is really a

compound organism, the alga being closely associated with a fungus to form a lichen-like thallus. In New Caledonia it was forming large masses several square inches in extent, and a few mms. high over mosses and tree-trunks. The thallus is bluish-green in colour, and seems to consist of a basal mat of anastomosing threads from all parts of which arise numerous tapering tufts

FIG. 1.



A. *Peronia erinacea* Bréb. & Arn., $\times 1423$. B-E. *Seytonema Hieronymi* Schmidle, $\times 510$. F. *Cymbella* sp., $\times 610$. G. *Euastrum intermedium* Cleve, f. *scrobiculata*, nov. f., $\times 510$. H-I. *Zygnema pectinatum* Ag., var. *decussatum* Kirchn. forma: H, $\times 350$; I, $\times 142$. J. *Stenopterobia intermedia* Lewis, var. *crassior*, var. nov., $\times 510$.

about 2 or 3 mm. high. Microscopic examination shows that it consists of a felt of *Scytonema* filaments bound together by anastomosing fungal hyphæ. The erect tufts also consist of a number of parallel *Scytonema* filaments closely adherent to each other, bound together and completely surrounded by a loose mat of hyphæ. The undulating lines in the sheath of the alga figured by Schmidle and thought by him to be due to the peculiar structure of the sheath itself, were very conspicuous also in the New Caledonian specimens, and after careful observation it was proved beyond all doubt that these undulating lines are caused by the hyphæ of the fungus, which are placed side by side round the algal filament to form a complete sheath. Further, the horizontal lines joining the undulating longitudinal lines are the septa of the hyphæ. The alga with its sheath of fungal hyphæ is seen in optical transverse section in text-fig. 1, C. The undulating arrangement of the hyphæ along the alga is most remarkable, and it is difficult at first to believe that the undulating lines are really due to a fungus, until at intervals irregularities may be observed, in which the hyphæ forming the sheath of the alga may separate from each other, and become apparent as ordinary hyphæ branching off into the ordinary free mycelium (text-fig. 1, D & E). At intervals also, the undulating hyphæ on the alga can be seen giving rise to branches, some of which may join up with the mat of mycelium which surrounds each bundle of algal filaments (text-fig. 1, B). Only those hyphæ forming the sheath of the *Scytonema* filament are wavy; the mycelium which is free from the alga consists of normal straight hyphæ. It is difficult to find a reason for the undulating nature of the hyphæ surrounding the alga, unless that by the hyphæ being thus dovetailed into each other, a stronger union is effected by them, and a firmer sheath results. It is noteworthy in this connection that the fungus sheath persists with violent treatment long after the enclosed *Scytonema* filament has disappeared, and that it breaks as a whole, transversely without the hyphæ showing any signs of separating from each other longitudinally. No trace of the fungal hyphæ actually penetrating the algal cells was observed. *Scytonema Hieronymi* seems to be a most interesting case of lichen formation.

SCYTONEMA DENSUM (A. Br.) Bornet. River Dumbéa; in small clear pool. 810. Europe, America.

S. ALATUM (Carm.) Borzi (*Petalonema alatum* Berk.). Forma trichomatibus gracilioribus, cellulis diametro circiter 3-plo longioribus ad apicem subquadratis. Mont Humboldt; on wet rocks or roots. 1045 b. Pic la; on wet serpentine soil. 865. Europe, America.

TOLYPOTHRIX BYSSOIDEA (Harv.) Kirchn. Specimen without locality. 88. Europe, Borneo, W. Indies.

STIGONEMACEÆ.

MASTIGOCOLEUS OBTUSUS, sp. nov. (Pl. 4. figs. 7-9.) *M.* filis inæqualibus, ramosissimis; ramis biformibus, his brevibus crassis, apice obtusus, illis longis flagelliformibus, sæpe ramosis; trichomatibus quam filum triplo angustioribus valde irregularibus et crassitudine inæqualibus; cellulis irregularibus subquadratis vel diametro longioribus, contentu pallide ærugineo; tegumento crasso inæquali, hyalino, hinc inde constricto, ibique lamellis latius divergentibus prædito, alibi homogæneo; ramulis flagelliformibus tenuiter et solide vaginatis nec manifeste septatis, heterocystis nullis. Diam. fil. 25-38 μ ; crass. trich. 4-14 μ ; long. cell. 9-30 μ ; long. ram. flagelliform. ad 800 μ ; crass. 2-7 μ .

Mont Canala; forming a thin, slimy, almost invisible film together with *Glæothecæ Vibrio* and *Rosaria ramosa* over excrescences on trees. 1181. This species is sufficiently distinct from the only other species of the genus by virtue of its thick hyaline sheath, and the irregular form of the cells and filaments. Furthermore, unlike *Mastigocoleus testarum* Lagerh., its whip-like branches, which may themselves be branched, are provided with a sheath throughout their whole length, and although the contents of these slender branches may be distinctly septate at the base, for the greater part of their length, septa cannot be distinguished. The complete absence of heterocysts is another noteworthy feature, and one which necessitates a revision of the generic description.

MASTIGOCOLEUS Lagerh., char. emend.

Fila libera irregulariter ramosa; articuli præter ramigeros unica cellula constantes. Rami biformes, partim cylindrici, partim flagelliformes in pilum attenuati. Vagina continua. Heterocystæ singulæ sæpe pedicellatæ rarissime binæ, terminales vel laterales, nunquam intercalares; interdum nullæ. Multiplicatio hormogoniis (et cellulis chroococcoideis?). Sporæ ignotæ. Contentus cellularum homogæneus.

ROSARIA, gen. nov.

Planta filis vere ramosis, cellulis moniliformibus uniseriatis, ramis ramulisque quaquaversus divergentibus, diametro filo subæqualibus, apicem versus leviter attenuatis, vagina plerumque nulla, heterocystis nullis.

ROSARIA RAMOSA, sp. nov. (Pl. 4. figs. 2-6.) *R.* filis longis ramosis plerumque evaginatis, ramis longioribus ramulisque præditis, cellulis ferme sphaericis membrana solida nec mucosa, contentu pallide ærugineo lucemque magnopere refringente, nonnullis magnis guttulis oleosis instructo; heterocystis nullis. Diam. cell. 13-19 μ ; long. cell. 19-22 μ .

Mont Canala; forming a very thin mucous film together with *Glæothecæ Vibrio* and *Mastigocoleus ramosus* over excrescences on the bark of trees. 1181. This is a peculiar and beautiful alga which looks like a string of

glistening pearls under the low power of the microscope. As regards its systematic position, it seems nearest to *Hapalosiphon*, differing chiefly in the absence of heterocysts, its irregular branching, and in the usual absence of the thin, firm sheath commonly present in that genus. Its branching is sparse and irregular, the branches arising in all directions, and branches of the second order being quite frequent. The branches make practically a right angle with the parent branch, and all the cells, both of the main axis and the branches, are similar to each other, becoming simply more slender towards the apex. The alga has striking characters which distinguish it from all others. It has a peculiar form of apical growth by the budding of the apical cell, and the continued growth of this small portion budded off until it is large enough to be cut off as a distinct cell (Pl. 4. figs. 4, 5). Very rarely a gelatinous sheath is present, or it may be represented by an almost invisible diffuent colourless mucus surrounding the filaments. Sometimes it apparently becomes firm and yellowish, and in this condition it often has a peculiar radiating structure which recalls the structure of the mucous sheath in certain filamentous Desmids (Pl. 4. fig. 6). The absence of heterocysts is peculiar, and in view of the fact that the significance of these cells is still not properly understood, it is noteworthy that the alga associated with *Rosaria ramosa*, namely *Mastigocoleus obtusus*, was also destitute of heterocysts, although in the other species of the genus *Mastigocoleus* heterocysts are present.

FISCHERELLA AMBIGUA (Näg.) Gom. Specimen without locality. 90. Europe, India, Sandwich Islands, America.

STIGONEMA HORMOIDES (Kütz.) Born. et Fla. Specimen without locality. 1092. Europe, Australia, America.

STIGONEMA sp. crass. fil. sine teg. $30\ \mu$; cum teg. $60\ \mu$; diam. cell. $8\ \mu$. Plaine des Lacs; in shallow rain pools. 338. The filaments were not infrequent; they were about 1 mm. in length, unbranched, and were probably in an imperfect state of development.

RIVULARIACEÆ.

RIVULARIA HÆMATITES (DC.) Ag. Pic La, incrusting rocks in trickle of water. 864. Europe, America.

BACILLARIÆ.

MELOSIRACEÆ.

MELOSIRA ITALICA Kütz. Mont Humboldt; with Blue-green algae on stones in rock pools. 1045 a.

CYCLOTELLA MENEGHINIANA Kütz. Canala ; in washings of *Azolla* from roadside ditch. 1359.

TABELLARIACEÆ.

TABELLARIA FLOCCULOSA Kütz., var. *VENTRICOSA* Grun. River Dumbéa ; amongst filamentous algæ. 809. Ouendjam Forest ; in washings from *Potamogeton* in slowly running stream. 1986.

DIATOMELLA BALFOURIANA Grev. Long. 9–14 μ ; lat. 3–4.5 μ . (Pl. 4. figs. 11–13.) River Dumbéa ; amongst filamentous algæ. 809. Mont Humboldt ; with Blue-green algæ in rock pools. 1045 a. The specimens agreed very well with the original figures of Greville (Ann. Mag. Nat. Hist. vol. xv. 1855, t. 9, figs. 10–13), but differed somewhat from those of later authors. For whereas this diatom is usually figured as linear-elliptic in the valve view, and slightly tumid in the middle, Greville's figures show an exactly linear-elliptic valve view without any trace of a median swelling. The New Caledonian specimens also were oval to elliptic in the valve view according to the size of the individual, without any median tumidity. The specimens further showed the presence in the valve view of a conspicuous median slit in the internal septum connecting longitudinally the three windows (Pl. 4. fig. 12). These slits do not seem to have been noted previously, yet it is strange that they should have been overlooked, since they are very conspicuous in the valve view. The raphe is a much more delicate structure which could not be confused with the slit, which it overlies. The raphe is only seen when the valve, without the septum, is separated from the frustule (Pl. 4. fig. 11). The diatom was particularly abundant in 1045 a.

DENTICULA ELEGANS Kütz. Plaine des Lacs ; in shallow rain pools. 338. River Dumbéa : amongst filamentous algæ in rock pools. 809. Mont Humboldt ; amongst Blue-green algæ in rock pools. 1045 a. River Ngoye ; amongst filamentous algæ in rock pools. 2411.

FRAGILLARIACEÆ.

SYNEDRA ULNA Ehrenb. Ermitage stream ; in pools. 176. Mont Dore ; in pool, littoral zone, at mouth of small stream. 852. Mont Canala ; amongst filamentous algæ in sluggish stream. 1242. Canala ; in washings of *Azolla* and *Lemna*, and amongst other algæ in streams and pools. 1356, 1357, 1359. Ouendjam Forest ; in washings of *Potamogeton* from slowly running stream. 1986.

S. ACUS Kütz. Canala ; in washings of *Azolla* in roadside ditch. 1359. Mont Dore ; in pool in littoral zone. 852.

MERIDIONACEÆ.

PERONIA ERINACEA Bréb. et Arn., forma. (Text-fig. 1, A.) Forma valvis a fronte visis non apice rostrato-capitatis, pseudoraphe vix conspicua. Ouendjam Forest. 1986. Very abundant amongst other diatoms in slowly running stream.

EUNOTIACEÆ.

EUNOTIA PRÆRUPTA Ehrenb. Canala ; in stagnant pool. 1358.

E. LUNARIS Grun. Rivière du Carénage ; amongst filamentous algæ. 384. Plaine des Laes ; in shallow rain pools. 338. Ouendjam Forest ; in slowly running stream. 1986.

E. IMPRESSA Ehrenb. Plaine des Laes ; in shallow rain pools. 338.

E. PECTINALIS Kütz. Canala ; in washings of *Lemna* sp. 1357. Ouendjam Forest ; in slowly running stream. 1986.

E. SOLEIROLII Rabenh. Mont Humboldt ; in rock pools. 1045 a. Only a single example of this species was noticed.

E. VENTRALIS Ehrenb. Ouendjam Forest ; in slowly running stream. 1986.

E. BICAPITATA Grun. Rivière du Carénage ; amongst other algæ in stream. 384.

ACHNANTHACEÆ.

ACHNANTHES MICROCEPHALA Kütz. River Dumbéa ; amongst filamentous algæ. 808, 809. Mont Humboldt ; amongst Blue-green algæ in rock pools. 1045 a. Europe.

A. HUNGARICA Grun. Canala ; in washings of *Lemna* sp. 1357. Europe.

A. TRINODIS Arn. River Dumbéa ; amongst filamentous algæ in rock pools. 808, 809. Europe.

A. LANCEOLATUM Grun. Ouendjam Forest ; in slowly running stream. 1986. Europe, Australia, New Zealand, India, America.

A. INFLATA Grun., var. *SMITHIANA* Grov. Ouendjam Forest, in slowly running stream. 1986. New Hebrides, Africa.

COCCONEIDACEÆ.

COCCONEIS PLACENTULA Ehrenb. Canala ; on dead leaves in pool. 1358. Ouendjam Forest ; in slowly running stream. 1986. Europe, New Zealand, America.

NAVICULACEÆ.

NAVICULA NOBILIS Ehrenb. River Dumbéa ; amongst filamentous algæ in rock pools. 809. Europe, America.

N. VIRIDIS Kütz. River Dumbéa. 809. Ouendjam Forest ; in slowly running stream. 1986. Europe, Australia, America.

N. MESOLEPTA Ehrenb., var. *THERMES* (Ehrenb.) Van Heurck. Ouendjam Forest. 1986. Europe, New Zealand.

N. LEGUMEN Ehrenb. Plaine des Lacs ; in shallow rain pools. 338. Ouendjam Forest. 1986. Europe, India, Australia, New Zealand, Japan, America.

N. RADIOSA Kütz., var. *TENELLA* (Bréb.) Van Heurck. Plaine des Lacs. 338. River Dumbéa ; amongst filamentous algæ in rock pools. 808, 809. Ouendjam Forest. 1986. Europe, Japan, Africa, America.

N. RHYNCOCEPHALA Kütz. Canala ; in pool. 1358. Europe, Australia, S. Africa, America.

N. BREVICOSTATA Cleve. Canala ; in pool. 1358. Europe, India.

N. SERIANS Bréb. Plaine des Lacs. 338. River Dumbéa. 809. Mont Humboldt ; with Blue-green algæ in rock pools. 1045 a. Europe, Australia, New Zealand.

N. EXILIS Grun. Plaine des Lacs. 338. Mont Humboldt. 1045 a. Europe.

N. IRIDIS Ehrenb., var. *AMPHIRHYNCHUS* (Ehrenb.). Canala ; in stagnant pool. 1358. Ouendjam Forest ; in slowly running stream. 1986. Europe, Australia, N. America.

N. PUPULA Kütz. Ouendjam Forest. 1986. Europe, Japan, India, Australia, New Zealand, S. Africa, S. America.

N. CONFERVACEA (Kütz.) Grun. Mont Canala ; in sluggish stream. 1242. Canala ; in pool and in ditch. 1358, 1359. India, Sandwich Islands, Australia, Jamaica.

STAURONEIS PHENIGENTERON Ehrenb. Ouendjam Forest ; in slowly running stream. 1986.

VANHEURCKIA RHOMBOIDES Bréb. Plaine des Lacs ; in shallow rain pools. 338. Var. *SAXONICA* Rabenh. (*Navicula crassinervia* Bréb.). Plaine des Lacs. 338. Europe, India, Australia, New Zealand, America.

V. VIRIDULA Bréb. Plaine des Lacs. 338. Europe.

MASTOGLOIA GREVILLEI W. Sm. River Dumbéa ; amongst submerged algæ in rock pools and amongst Blue-green algæ in gelatinous layer incrusting dripping rocks. 809, 811. Europe.

PLEUROSIGMA ELONGATUM W. Sm. Canala ; abundant amongst filamentous algæ in fairly swift stream, and in pool. 1356, 1358. Europe, China, Malaya, America.

GOMPHONEMACEÆ.

GOMPHONEMA INTRICATUM Kütz. Plaine des Laes. 338. Ouendjam Forest ; abundant in slowly running stream. 1986. Var. *VIBRIO* (Ehr.) Van Heurck. Ouendjam Forest ; abundant. 1986. Europe, America.

G. SUBCLAVATUM Grun. Mont Canala ; in sluggish stream. 1242. Canala ; in washings of *Azolla* from roadside ditch. 1359. Europe, Australia, New Zealand, Sandwich Islands, America.

COCCONEMACEÆ.

CYMBELLA OBTUSA Greg. Plaine des Laes ; in shallow rain pools. 338. River Dumbéa. 809. Ouendjam Forest ; in slowly running stream. 1986. Europe, America.

C. TUMIDA Bréb. Mont Canala ; in sluggish stream. 1242. Canala ; in washings of *Azolla* in roadside ditch. 1359. Ouendjam Forest ; in slowly running stream. 1986. Europe, China and Japan, India, Australia, New Zealand, America.

C. TURGIDA Greg. Canala ; in pool. 1358. Europe, Malaya, Australia, New Zealand, America.

C. CESATH Grun. River Dumbéa ; amongst filamentous algæ. 808. Europe, Canada.

? *CYMBELLA* sp. (Text-fig. 1, F.) River Dumbéa. 808, 809. Mont Humboldt. 1045 a. Ouendjam Forest. 1986. This naviculoid diatom was present in great abundance in several of the collections. In 1045 a it was forming auxospores in great numbers, and the frustules varied exceedingly in size. The valves are practically symmetrical, and it is possibly a *Navicula*, but a few of the median striae on one side always seem to end with a rather distant and more distinct punctum than those on the other side. Because of this asymmetry I have referred it to *Cymbella*, but have not been able to decide on its exact identity. The broad axile area and the fine striation with its linear-lanceolate form are quite characteristic. The striae are punctate, and there are about 16 in 10 μ .

AMPHORA OVALIS Kütz. Ouendjam Forest; in slowly running stream. 1986. Var. *GRACILIS* (Ehr.) Van Heurck. Mont Dore; in pool in littoral zone. 852. Europe, Australia.

EPITHEMIA ARGUS Kütz. Rivière du Carénage. 384. River Dumbéa. 808, 809.

E. ZEBRA (Ehr.) Kütz. Mont Canala; in sluggish stream. 1242. Canala; in pool and ditch. 1358, 1359. Ouendjam Forest; in stream. 1986. Var. *PORCELLUS* Grun. Canala. 1358.

E. REICHELTII Fricke, Schmidt Atlas, t. 251, f. 28-32. Mont Canala. 1242, 1356. Ouendjam Forest. 1986.

RHOPALODIA GIBBA O. Müll. Mont Canala. 1242, 1359. Ouendjam Forest. 1986.

R. VENTRICOSA O. Müll. Canala. 1357, 1358.

NITZSCHIACEÆ.

NITZSCHIA TRYBLIONELLA Hantzsch. Ouendjam Forest. 1986.

N. SIGMA W. Sm. Canala. 1358.

N. LINEARIS (Ag.) W. Sm. Mont Mou; in stream. 528. Mont Dore; in pool in littoral zone. 852. Canala. 1358.

N. AMPHIBIA Grun. Ouendjam Forest. 1986.

SURIPELLACEÆ.

SURIPELLA BISERIATA Bréb. Ouendjam Forest. 1986.

S. LINEARIS W. Sm. Canala. 1356. Ouendjam Forest. 1986.

S. SPLENDIDA Kütz. (*S. robusta* var. *splendida* Van Heurck). Mont Dore; in pool in littoral zone. 852.

STENOPIEROBIA INTERMEDIA Lewis, var. *CRASSIOR*, var. n. (Text-fig. 1, J.) Var. *valvis multo brevioribus et pro ratione crassioribus, utrinque subcuneatis, striis ut in typo.* Long. 265μ ; lat. 19μ . Rivière du Carénage. 384. Frequent.

CYMATOPLEURA SOLEA (Bréb.) W. Sm. Ouendjam Forest. 1986.

CHLOROPHYCEÆ.**PAIMELLACEÆ.**

GLÆOCYSTIS GIGAS (Kütz.) Lagerh. Canala. 1359. Europe, India, America.

AUTOSPORACEÆ.

OOCYSTIS PARVA W. & G. S. West. River Dumbéa. 809. Europe.

SCENEDESMUS BIJUGATUS (Turp.) Kütz. Plaine des Lacs. 338. Canala. 1359. Ubiquitous. Var. *ALTERNANS* (Reinsch) Borge. Plaine des Lacs. 338.

S. OBLIQUUS (Turp.) Kütz. Canala. 1359. Ubiquitous.

SORASTRUM SPINULOSUM Nüg. Canala. 1359. Europe, India, New Zealand, America.

HYDRODICTYACEÆ.

PEDIASTRUM TETRAS (Ehrenb.) Ralfs. Canala. 1359. Plaine des Lacs. 338. Ubiquitous.

CLADOPHORACEÆ.

RHIZOCLONIUM HIEROGLYPHICUM Kütz. With *Nitella hyalina*, No. 638.

ULOTRICHACEÆ.

ULOTRICH SUBTILIS Kütz. Plaine des Lacs. 338. Var. *VARIABILIS* (Kütz.) Kirchn. Plaine des Lacs. 338.

CHÆTOPHORACEÆ.

STIGEOCLONIUM FARCTUM Berth. Mont Canala. 1242. The alga was very abundant as an epiphyte on the hairs of a flowering plant which had evidently fallen into the stream and become covered with algæ. In many cases the apical cells of the short erect branches were very turgid and swollen, apparently just about to produce zoogonidia. Germany.

PROFODERMA VIRIDE Kütz. Mont Canala. 1242. Epiphytic on hairs of fallen submerged plant. 1159. Epiphytic on *Nitella* sp.

ENDODERMA POLYMORPHA G. S. West, West Ind. Freshw. Alg. 1904, p. 283. t. 464, f. 19. Mont Canala. 1242. Epiphytic on hairs of fallen submerged plant. 1159. On *Nitella* sp. West Indies.

The plants were more compact and the cells somewhat smaller on the hairs of the plant than those growing on the huge segments of *Nitella* sp. in 1159. There were occasional evidences of zoogonidia formation in 1242.

TRENTEPOHLIACEÆ.

TRENTEPOHLIA AUREA (L.) Mart. Mont Mou ; incrusting rocks in slight shelter. 612. Europe, America, New Zealand, Sumatra.

T. VILLOSA (Kütz.) De Toni. Ermitage Stream ; in pendent tufts on dead trunks over stream. 193. Not common. Brazil, West Indies, Sumatra.

T. DIALEPTA (Nyl.) Hariot, Schmidle, Alg. aus Neu-Guinea, 1897, p. 306. Ermitage Stream ; bright green spongy masses and small brackets projecting from twigs and branches over stream. 151. New Guinea. The thalli were somewhat smaller than those described by Schmidle from New Guinea, being at the most 3 cm. in diameter, and the plates only 1 mm. thick. The fungal hyphæ in the wall of the alga were clearly visible with fairly high magnification, and occasionally spores were produced in connection with the hyphæ. Apothecia, however, were not present, neither was the alga itself fruiting.

? T. POLYCARPA Nees & Mont. Mont Koghi ; forming an orange filamentous covering to serpentine rocks in a stream-course. 757. (Probably this species, but owing to absence of reproductive cells, exact identity uncertain.)

CEPHALEUROS VIRESCENS O. Kuntze (*Mycoidea parasitica* Cunn. ; *Strigula complanata* Fée). 563. On leaves. America, India, Java.

APHANOCHÆTACEÆ.

APHANOCHÆTE HYALOTHECÆ Hansg., var. MUCICOLA Schmidle in Weit. Beitr. Alg. Rheineben &c. 1895, p. 67. Canala ; from washings of *Azolla* sp. in ditch. 1359 On *Hyalotheca dissiliens*. The plants bore large oval oospores, but no antheridia were observed. Germany.

COLEOCHÆTACEÆ.

COLEOCHÆTE ORBICULARIS Pringsh. Mont Canala. On hairs of fallen plant in sluggish stream. 1242. Europe, America, New Zealand.

ZYGNEFACEÆ.

MOUGEOTIA SCALARIS Hass. Plaine des Lacs ; in shallow rain pools. 338. Europe, America, Australia.

Sterile species of *Mougeotia* occurred in Nos. 338, 384, 809, 1356, 1359, 1986, 2411.

ZYGNEMA PECTINATUM (Vauch.) Ag., var. DECUSSATUM (Vauch.) Kirchn. Forma conjugatione laterali. (Text-fig. 1, H & I.) Crass. fil. veg. 13-16 μ ; diametro 5-plo longioribus ; diam. zyg. 30-35 μ .

Plaine des Lacs ; in shallow rain pools. 338. Rivière du Carénage ; on rocks in stream. 384. Europe, America. This alga agrees almost

exactly with *Z. rhyrachonema* Hansg., differing only in the scrobiculate middle wall of its zygote. In this latter character it is nearer to *Z. pectinatum*, and for this reason has been referred to the variety *decussatum* of that species, which it resembles very much in its slender filaments and longer cells. The zygospores, however, were usually formed in the conjugation tube by lateral conjugation instead of by scalariform conjugation, as is usual in that species. The latter form of conjugation occurred very occasionally, and only as a great exception. Lateral conjugation in typical *Z. pectinatum* has, however, already been reported by Fritsch & Stephens in Trans. Roy. Soc. South Africa, vol. ix. 1921, p. 53, fig. 24.

Sterile species of *Zygnema* occurred in Nos. 338, 384, 1356, 1986.

SPIROGYRA COMMUNIS (Hass.) Wittr. Mont Canala; in sluggish stream. 1242.

Sterile species of *Spirogyra* occurred in Nos. 176, 384, 528, 852 (with unripe zygospores), 1242, 1356, 1359.

DESMIDIACEÆ.

GONATOZYGON MONOTÆNIUM De Bary. Canala; in washings of *Azolla* from slowly running water in ditch. 1359. Europe, America, India, Malaya. Var. *PILOSELLUM* Nordst. Canala; in fairly swift stream amongst *Spirogyra* sp. 1356. Ireland, Brazil.

G. KINAHANI (Archer) Rabenh. Rivière du Carénage; amongst algæ attached to rocks. 384. Europe, America, Malaya. Forma major, pyrenoidibus numerosissimis. Long. cell. $660\ \mu$; lat. $18\ \mu$. Rivière du Carénage. 384.

CYLINDROCYSTIS BREBISSENI Menegh. Plaine des Lacs; in shallow rain pools. 338. Rivière du Carénage. 384. Europe, India, Malaya, Australia, New Zealand, E. Africa, America.

NETRIUM DIGITUS (Ehrenb.) Itzigs. & Rothe. Plaine des Lacs. 338. Europe, China and Japan, India, Malaya, Australia, New Zealand, America. Var. *CONRICTUM* W. & G. S. West. Rivière du Carénage. 384. Europe.

PENIUM MARGARITACEUM (Ehrenb.) Bréb. Ouendjam Forest; in slowly running stream. 1986. Europe, Java, New Zealand, E. Africa, America. The specimens were much more rounded at the extremities than usual, and were provided with a large, conspicuous terminal vacuole at each end.

P. MINUTISSIMUM Nordst. (Pl. 4. fig. 15.) Plaine des Lacs. 338. Europe, Burma, Siam, Madagascar, S. America. The specimens were slightly longer and narrower. Long. $17\ \mu$; lat. $8\ \mu$. Zygospores were not uncommon.

CLOSTERIUM PSEUDODIANÆ Roy. Canala; in washings of *Azolla* sp. from roadside ditch. 1359. Europe, Ceylon, Madagascar, E. Africa.

C. VENUS Kütz. Canala: in washings of *Azolla* sp. from roadside ditch. 1359. Europe, China and Japan, India, Malaya, New Zealand, Africa, America.

C. LEIBLEINII Kütz. Ouendjam Forest; in slowly running stream. 1986. Europe, Japan, India, Australia, Africa, America.

C. MONILIFERUM (Bory) Ehrenb. Ermitage Stream. 176. Canala; in stream, in stagnant pool, and in ditch. 1356, 1357, 1359. Europe, China and Japan, Ceylon, New Zealand, Africa, America. Forma *INTERMEDIA* Gutw. Canala; in ditch. 1359. Europe.

C. EHRENBERGII Menegh. Canala; in stream and ditch. 1356, 1359. Ouendjam Forest; in slowly running stream. 1986. Europe, China and Japan, India, Malaya, New Zealand, Africa, America.

C. ACEROSUM (Schrank) Ehrenb. Ouendjam Forest; in slowly running stream. 1986. Europe, Siberia, China and Japan, India, Malaya, Australia, New Zealand, America.

C. PERACEROSUM F. Gay. Canala; in washings of *Azolla* in ditch. 1359. France, W. Africa.

C. KUTZINGII Bréb. Canala; in pond and in ditch. 1357, 1359. Europe, India, Malaya, Australia, New Zealand, C. Africa, America.

C. COMPACTUM Nordst. Plaine des Lacs; in shallow rain pools. 338. New Zealand.

PLEUROTÆNIUM MAXIMUM (Reinsch) Lund. Plaine des Lacs. 338. Europe, Ceylon, Malaya, Africa, America. Forma *cellulis gracilioribus*. Long. cell. 720μ ; lat. 30μ . Canala; in ditch. 1359.

P. BASIUNDATUM W. & G. S. West. Canala; in ditch. 1359. Madagascar, Australia. The form was similar to that figured by Borge (Austral. Süßwasserchlorophyceen, 1894, p. 26, t. 3, f. 46). The original figure of West does not show any apical nodules, whilst that of Borge does. In the New Caledonian specimens the nodules were small and not conspicuous, but they could usually be distinguished. The basal inflation of the semicell was also smaller than that figured by West.

P. SUBGEORGICUM Cushman in Rhodora, 1905, p. 117. Canala; in ditch. 1359. United States. The apical tubercles were not constantly present, but were sometimes quite distinct.

TETMEMORUS LÆVIS (Kütz.) Ralfs. Plaine des Lacs ; in shallow rain pools. 338. Europe, Malaya, Australia, New Zealand, America.

EUASTRUM DENTICULATUM (Kirchn.) Gay. Plaine des Lacs. 338. Europe, China, Malaya, Australia, New Zealand, Africa, America.

E. PECTINATUM Bréb. River Dumbéa ; amongst other algæ in rock pools. 809. Europe, America.

E. INSULARE (Wittr.) Roy. Plaine des Lacs. 338. Northern Europe, Siam, United States.

E. INTERMEDIUM Cleve, forma **SCROBICULATA**, n. f. (Text-fig. 1, G.) Canala ; in ditch. 1359. The alga was not common. In form it is very near *Eu. intermedium*, differing chiefly in its scrobiculate cell-wall and larger lateral lobes. It is very similar also to *Eu. orientale* W. B. Turn. (Freshw. Alg. E. India, p. 79, t. 10, f. 34, t. 11, f. 26), but differs in the polar lobe, which in Turner's species, as in *Eu. insigne*, is 4-lobed, whilst in *Eu. intermedium* it is 2-lobed.

MICRASTERIAS DECEMDENTATA Nügg. formæ. Canala ; in ditch. 1359. The specimens were numerous and very variable, all intermediate stages between two extreme forms being present. One of these forms was identical with that figured by Schmidle (Süsswasseralgen aus Australien, 1896, p. 310, t. 9, f. 18), and also by Playfair as *M. truncata* (Corda) Bréb., var. *decemdentata* Playfair (Some Sydney Desmids, 1908, p. 608). The other form was also figured by Playfair (*ibid.* t. 9, ff. 8-9) as *M. truncata* var. *laticipiformis* Playfair. The dimensions of the specimens from Canala were : long. 88-110 μ ; lat. 108-116 μ .

COSMARIUM LUNDELLII Delp., forma. Rivière du Carénage. 384. Rare. The cells were small and very depressed, being slightly broader than long. Long. 47 μ ; lat. 56 μ ; crass. 27 μ .

COSMARIUM PHASEOLUS Bréb. Plaine des Lacs ; in shallow rain pools. 338. Europe, India, Australia, New Zealand, Africa, America.

C. ASPHÆROPHORUM Nordst. Plaine des Lacs ; in shallow rain pools. 338. Europe, New Zealand, United States.

C. CONTRACTUM Kirchn. Plaine des Lacs. 338. Europe, Malaya, Australia, Africa, America.

C. HAMMERI Reinsch. Plaine des Lacs. 338. The form of the cells was similar to that figured by Borge (Alg. erst. Regnel. Exp. 1903, t. 3, f. 17) from Brazil.

COSMARIUM TRILOBULATUM Reinsch. Plaine des Lacs. 338. Europe, New Zealand, Africa, Brazil.

C. SUBTUMIDUM Nordst., var. *KLEBSII* (Gutw.) W. & G. S. W. River Dumbéa ; amongst other algæ in rock pools. 809. Europe.

C. ARCTOUM Nordst. Plaine des Lacs. 338. Europe, New Zealand.

C. MENEGHINII Bréb. Plaine des Lacs. 338. Mont Canala ; in sluggish stream. 1242. Ubiquitous.

C. DIFFICILE Lüttk. River Dumbéa ; amongst other algæ in rock pools. 809. Europe, United States.

C. CUCURBITA Bréb. Rivière du Carénage. 384. Europe, Singapore, Australia, Africa, America.

C. TURGIDUM Bréb. Canala ; in washings of *Azolla* sp. in ditch. 1359. 638. Europe, Japan, Australia, New Zealand, Patagonia.

C. SUBTURGIDUM (W. B. Turn.) Schmidle. Canala ; in ditch. 1359 (and forma *MINOR* Schmidle). 638. India, Malaya, Australia, Africa.

C. QUADRIFARIUM Lund. Plaine des Lacs. 338. (Formæ *hexasticha* (Lund.) Nordst. and *octasticha* Nordst.) Europe, Ceylon, Java, New Zealand, S. America.

C. WITTROCKII Lund. River Dumbéa. 809. Plaine des Lacs. 338. Europe, Siam, Patagonia.

C. PUNCTULATUM Bréb. Canala ; in ditch. 1359. Europe, China and Japan, India, Malaya, Australia, New Zealand, Africa, America.

C. BINUM Nordst., var. *ANGUSTATUM*, var. n. (Pl. 4. fig. 10.) Var. cellulis diametro fere duplo longioribus, semicellulis truncato-pyramidatis, crenis lateralibus inferioribus singulis tantum granulis præditis, superioribus emarginatis. Long. cell. 54μ ; lat. 29μ . River Dumbéa. 808, 809.

C. CUCURBITINUM (Bisset) Lüttk. (*Penium cucurbitinum* Biss.), var. *SUBPOLYMORPHUM* Nordst. Rivière du Carénage. 384. Austria, New Zealand.

C. CRUCIFERUM De Bary. Plaine des Lacs. 338. Europe, New Zealand, Africa, United States.

COSMARIUM DOCIDIODES Lütke. (*Penium minutum* (Ralfs), Cleve), forma MAJOR Lund. Rivière du Carénage. 384. Europe. Var. GRACILE Wille. Plaine des Laes. 338. Europe, Africa, America.

STAUSTRUM ORBICULARE Ralfs, var. *DEPRESSUM* Roy & Biss. (Pl. 4. fig. 14.) Canala; in ditch. 1359. Europe, China and Japan, Siam, Australia, New Zealand, Madagascar. The specimens were typical in size and form, but the cell-wall often showed a slight thickening, usually at the angles and sometimes at the apex of the semi-cell as well.

S. ALTERNANS Bréb. Canala; in ditch. 1359. Europe, India, Siam, Australia, New Zealand, Africa, United States.

S. INFLEXUM Bréb. River Dumbéa. 809. Europe, Japan.

HYALOTHECA DISSILIENS (Sm.) Bréb. Canala; in ditch. 1359. Europe, China, India, Malaya, Australia, Africa, America.

H. NEGLECTA Racib. Plaine des Laes. 338. British Isles, Ceylon, United States, Guiana. The specimens were very large. Long. cell. $55\ \mu$; lat. max. $15\ \mu$.

DESMIDIUM BAILEYI (Ralfs) De Bary, var. *UNDULATUM* (Mast.) Nordst. Canala; in ditch. 1359. Java, Australia.

ÆDOGONIACEÆ.

BULBOCHÆTE ELATIOR Pringsh. Plaine des Laes. 338. Europe, India, Australia. Sterile species of *Bulbochæte* occurred in Nos. 812 and 338.

ÆDOGONIUM OBLONGUM Wittr. Plaine des Laes. 338. Europe, India, Australia.

ÆDOGONIUM sp. Plaine des Laes. 338. This species was fruiting, but the oospores were very young. It is monœcious, and is peculiar in that the oogonium opens with a pore which is distinctly beneath the median part. Thus it does not seem to be identical with any described species. It differs from *O. inversum* Wittr. in being monœcious and in opening with a pore, and from *O. cryptoporum* Wittr. in the more inferior position of the pore and relatively longer cells.

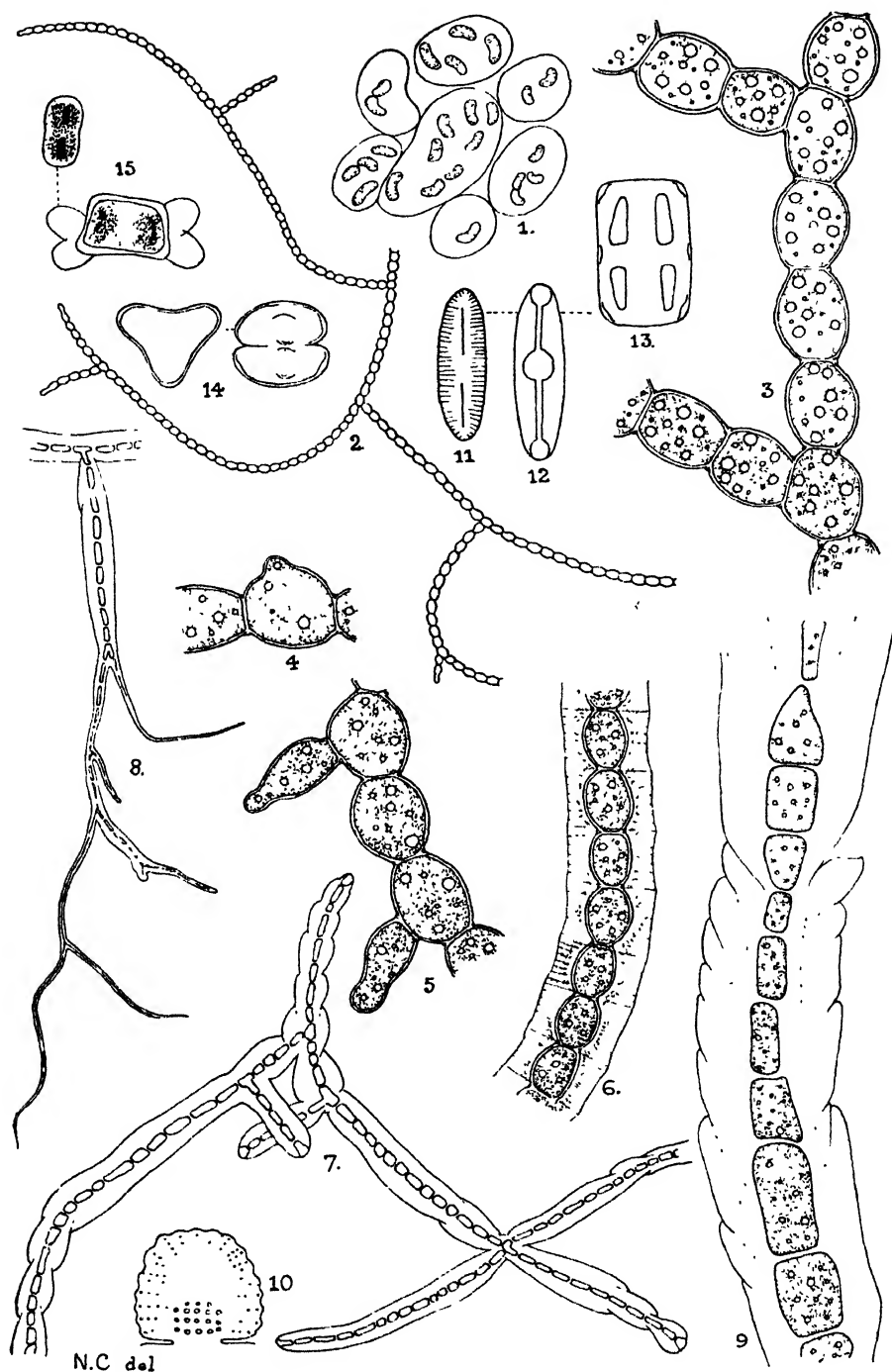
Sterile species of *Ædogonium* occurred in Nos. 338, 384, 638, 812, 852, 1242, 1359, and 1986.

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EXPLANATION OF PLATE 4.

- Fig. 1. *Glaucotheca Fibrio*, sp. nov., $\times 810$.
- Figs. 2-6. *Rosaria ramosa*, sp. et gen. nov. Fig. 2, $\times 78$; figs. 3-6, $\times 510$.
- 7-9. *Mastigocoleus obtusus*, sp. nov. Figs. 7 & 8, $\times 92$; fig. 9, $\times 510$.
- Fig. 10. *Cosmarium binum* Nordst., var. *angustatum*, var. nov., $\times 510$.
- Figs. 11-13. *Diatomella Balfouriana* Grev., $\times 1423$.
- Fig. 14. *Staurastrum orbiculare* Ralfs, var. *depressum* Roy, $\times 510$.
15. *Penium minutissimum* Nordst., $\times 510$.



FRESHWATER ALGÆ FROM NEW CALEDONIA.

CHAROPHYTA.

By JAMES GROVES, F.L.S.

(PLATE 5.)

NITELLA PSEUDO-FLABELLATA Braun in Braunn & Nordstedt, Fragm. Monogr. Charac. 54 (1882)? Dumbéa; muddy ditch; on serpentine rock; 100 ft. April 1914. 812 (part).

In the absence of ripe fruit, I can only refer this doubtfully to *N. pseudo-flabellata*, itself an indefinite species which has never been properly diagnosed. From Braun's remarks in the 'Fragments,' it is evident that he was by no means satisfied as to the identity of the several plants which he had placed under the name.

N. COMPTONII, sp. nov. (Pl. 5.)

Sect. *Arthrodictyle* *homoclema* *macrodictyle* *flabellatæ* *glocephalæ* *monoicæ*.

Caulis tenuis c. 400 μ crassus. *Ramuli* normaliter 8, 3-4-plicato furcati, nodo infimo fere semper sterili. *Radius* primarius ramulæ totam longitudinem dimidio æquans. *Radii* secundarii 6-8; tertiarii 5-7, omnes vulgo iterum furcati; quarternarii 5-6, quorum 1-2 sæpe iterum furcati; quinarum 4-6. *Radii* ultimi bicellulati elongati tenues (crass. 40-50 μ) leviter incurvati, cellulâ inferiore ad apicem plus minusve angustatâ, cellulâ superiore elongato-conicâ acutâ \rightarrow 85 μ longâ, ad basem c. 25 μ crassâ. *Verticilli* fertiles in muco involuti, capitulas rotundas parvas sæpe formantes. *Oogonia* et *antheridia* ad furcas secundas et tertias posita. *Oogonia* solitaria ovoidea, ad basem aliquatenus, versus apicem insigniter, angustata, c. 400-450 μ longa (coronulâ exclusâ), 300-325 μ lata, convolutiones c. 10 exhibentes. *Coronula* persistens, c. 35 μ alta, 50 μ lata. *Oospora* ellipsoidea, c. 300 μ longa, 250 μ lata, 190 μ crassa, atrofusca, liras prominentes c. 8 exhibens; membrana subtiliter granulata. *Antheridium* diametro c. 250 μ .

Dumbéa; muddy ditch; on serpentine rock; 100 ft. April 1914. 812 (part). Baie Ba; on mica-schist alluvium; sea-level. July 1914. 1401.

A small, slender, dark-green plant, apparently not more than three or four inches high. The outstanding points of difference between the other species of the group and *N. Comptonii* may be summarised as follows:—*N. batrachosperma* Braun differs in the branchlets being only twice furcate, with the lowest node fertile and in the much smaller antheridium; *N. minuta* Allen, in the lower cell of the ultimate rays being rounded at the apex and the upper cell remarkably narrow, and in the fewer (6) and more pronounced ridges of the oospore; *N. leptosoma* Nordst., in the branchlets being only twice furcate, with the lowest node fertile, and in the fertile whorls being disposed in short, interrupted spikes; *N. intermedia* Nordst., in the uniformly

lax fruiting whorls, the branchlets not more than thrice furcate, with the lowest node fertile; *N. Asagrayana* Braun & Nordst., in the fewer (5-6) usually not more than twice furcate branchlets and the smaller ($170\ \mu$) antheridia; *N. pseudo-flabellata* f. *mucosa* Nordst., in the branchlets being only twice or thrice furcate, the broader nearly spherical oogonia, the larger dark red oospores showing fewer ridges, and the larger antheridia; *N. conformis* Nordst., in the short branchlets, only twice furcate with stout ultimate rays, and in the much larger antheridia ($350\ \mu$).

NITELLA HYALINA Agardh, Syst. Alg. 126 (1824), emend. Kützinger, Phyc. Germ. 256 (1845).

Tiaré, near Païta; pools and eddies in stream; on Triassic rock; 250 ft. March 1914. 638. Forming dense dark green masses in a stream at Taom; on serpentine rock; 200 ft. December 1914. 2292.

N. GELATINOSA Braun, Charac. Austral. & Antaret. in Hooker's Journ. Bot. i. 198 (1849). ♂ & ♀.

Isle of Pines; rooting in mud in a small stream at the entrance to a cavern, Omagu; on emerged coral rock. Nov. 1914. 2279.

A form with tapering, acute, ultimate cells to the rays, resembling those of *N. tasmanica*, but with small-stalked capitula. The sterile branchlets are furcate with fairly long secondary rays.

CHARA AUSTRALIS R. Brown, Prodr. Fl. Nov. Holl. & Ins. Van Diem. i. 346 (1810).

In a tributary of Rivière de Canala, Mont Canala; on mica-schist; 800 ft. June 1914. 1159. The female plant.

C. GYMNOPTYS Braun in Linnaea, xxv. 708 (1852).

Nouméa, Valley of Montravel; in a small stagnant well; on Triassic conglomerate; 50 ft. Jan. 1914. 16.

EXPLANATION OF PLATE 5.

Nitella Comptonii, sp. nov..

Fig. 1. Whorl, $\times 3$.

2. Single branchlet and capitulum enveloped in mucus, $\times 6$.

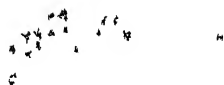
Figs. 3-6. Ultimate cells of dactyls, $\times c. 150$.

Fig. 7. Oogonium, $\times c. 65$.

8. Oospore, $\times c. 65$.

9. Membrane of oospore, $\times 480$.

Figs. 1-8, M. Groves, del.; Fig. 9, G. R. Bullock-Webster, del.



1

2



3

8

9



McCoy
highly ill

Chick
mp

NITELLA COMPTONII Groves

LICHENS.

By A. LORRAIN SMITH, F.L.S.

MR. COMPTON collected about 120 specimens of lichens. A certain number were sterile or otherwise undeveloped, but altogether 110 species or varieties have been recognized; of these, one genus and 20 species are new to science.

Several lists of lichens from New Caledonia have been published. In 1861, Nylander issued his "Expositio Lichenum Novæ Caledoniæ,"* which comprises 104 species. This was followed in 1868 by the "Synopsis Lichenum Novæ Caledoniæ,"† with 220 species or varieties. Müller-Aargau at a later date described 73 lichens from Nouméa‡, and more recently 127 different forms from N. Caledonia§.

About half of those brought home by Mr. Compton were already recorded in one or other of these lists, but as all of the collections vary considerably, we may conclude that the lichen-flora of New Caledonia is not yet exhausted.

Our knowledge of lichens—more especially of tropical lichens—is too fragmentary to allow of wide statements on distribution; but enough is known to draw some general conclusions. A number of lichens are cosmopolitan; a very large number are common to tropical and subtropical lands; a few, so far as is known, are endemic in different areas. New Caledonia lichens are closely allied to those of Oceania: Stictaceæ are well represented; genera such as *Thysanothecium* and *Heterodea* and species such as *Cladonia retepora* are confined to Oceania and are abundant on the island. Müller-Aargau, from his study of Nouméa lichens, concluded that air-currents transported the lichens of S. America to Africa, and thence to Oceania. The present collection certainly confirms that view. *Leptotrema* and *Lepidocollema* were until now monotypic genera confined to S. America: a second species of the former has appeared in New Caledonia, and a new genus, *Lepidoleptogium*, very closely allied to *Lepidocollema* has been diagnosed. Portions of lichen thalli are not only very light but support prolonged desiccation, and would revive after long sojourn in the air. The wide distribution of lichens is therefore not to be wondered at: the areas of distribution are climatic rather than geographical.

The specimens from New Caledonia submitted to me were mostly numbered, with a corresponding list of numbered localities. There was also a box containing sundry unnumbered rock specimens from Mont Montravel, north of Nouméa, and there were parcels of specimens from Baie Ouémo, Nouméa, also without numbers. I have to thank Dr. Bernt Lynge, Mr. Gepp, and Miss Wakefield for helpful suggestions.

* Ann. Sci. Nat. (Bot.), xv. 1861, 37-54.

† Bull. Soc. Linn. Norm. sér. ii. 1867 (1868), 39-140.

‡ Rev. Mycol. xxxiii. 1887, 77-82.

§ Journ. de Bot. vii. 1893, 51-55, 92-94, 106-111.

PYRENOCARPINEÆ*.

PYRENULACEÆ.

PYRENULA NITIDA Ach. Syn. Lich. 125, 1814. On bark of *Exothecca*. Baie Ouémo. Riv. Ngoyé, May. "Tree-trunks in *Spermolepis* forest on serpentine soil by river, 350 ft." 1102. Cosmopolitan.

Both specimens are untypical.

ANTHRACOTHECIUM DENUDATUM, var. OCHROTROPUM (Nyl.), Müll.-Arg. Lich. Neo-cal. in Journ. de Bot. vii. 111, 1893. On wood. 1295 bis. S. America.

The variety is distinguished by a yellow or reddish tinge over the normally white thallus. The yellow parts give a strong reaction, KHO + crimson, and this suggests that the thallus may be invaded by some other species. Wainio found the same lichen in Brazil, and placed it in a new genus, *Bottaria* (Trypetheliaceæ), with specific rank. As the perithecia are solitary, I have preferred to classify it as above.

TRYPETHELIACEÆ.

TRYPETHELIUM SPRENGELII Nyl. Exp. Syn. Pyrenoc. in Maine & Loire Mém. Soc. Acad. iv. 77, 1858. On bark of *Exothecca*. Baie Ouémo, near Nouméa. Universal in tropical and subtropical countries.

ASTROTHELIACEÆ.

ASTROTHELIUM SULPHUREUM Nyl. Prodr. Fl. Novo-Gran. in Ann. Sci. Nat. sér. 4, xx. 260, 1863. On bark. Riv. Ngoyé, May. "Tree-trunks in *Spermolepis* forest on serpentine soil by river, 350 ft." 1104. S. America.

GYMNOCARPEÆ.

SPHÆROPHORACEÆ.

SPHÆROPHORUS COMPRESSUS Ach. Meth. Lich. 135, 1803. 718, 1728. No. 718. "Abundant on trunks above 3500 ft. in cloud forest." Frequent in the Southern Hemisphere. The thallus in both of the specimens is ochreous-white, almost as if bleached; described by Compton as "white, with stout white erecto-patent apothecia stalks and black apothecia."

GRAPHIDACEÆ.

OPEGRAPHA DIAGRAPHA Nyl. Syn. Lich. N. Caled. 57, 1868. On bark of unknown tree. Baie Ouémo, Nouméa.

When moist the discs are brownish—not white as in Nylander's description; but this may be the result of age. The lirellæ are very short, resembling those of *O. Bonplandia* var. *abbreviata* Müll.-Arg.

* The arrangement followed is in general that of A. Zahlbruckner in Engler and Prantl's 'Natürlichen Pflanzenfamilien.'

GRAPHIS SUBCONTEXTA Nyl. Syn. Lich. N. Caled. 79. On bark of a tree. Riv. Ngoyé, May. "In *Spermolepis* forest on serpentine soil by river, 350 ft." 1098. New Zealand.

G. SCRIPTA Ach. Lich. Univ. 265, 1810. On bark of *Ficus*. Baie Ouémo, Nouméa. Cosmopolitan.

G. ELEGANS Ach. Syn. Lich. 85, 1814. On bark of *Exothea*. Baie Ouémo, Nouméa. Cosmopolitan.

The specimen is a very small one, and the furrows on the margins of the lirellæ are somewhat indistinct.

GRAPHINA MENDAX (Nyl.) Müll.-Arg. in Journ. de Bot. vii. 108, 1893; var. BISPORA A. L. Sm. On bark of unknown tree. Baie Ouémo, Nouméa.

Nylander and Müller-Aargau have both recorded the species from New Caledonia as with one spore in the ascus, $80-100\ \mu \times 26-38\ \mu$. In the specimen examined the spores are occasionally solitary and measure up to $100\ \mu$ in length; more frequently there are two spores in the ascus of smaller size, $57-80\ \mu \times 30\ \mu$.

CHIODECTONACEÆ.

GLYPHIS CICATRICOSA (Ach.) A. Zahlbr. in Engl. & Prantl, Nat. Pflanz.-Fam. 1, 1*, 103, 1905 (syn. *G. favulosa* Ach.). On bark of *Exothea*. Baie Ouémo, Nouméa.

Frequent in tropical and subtropical regions.

CHIODECTON SANGUINEUM (Sw.) Wain. Lich. Brés. ii. 143, 1890; *Ch. rubroinctum* (Ehrenb.) Nyl. Lich. Nov. Gran. 486, 1863. On bark. Riv. Ngoyé, 25th May. "In *Spermolepis* forest on serpentine soil by river, 350 ft." 1091. S. America, Africa.

CHRYSOTHRICACEÆ.

CROCYNIA GOSSYPINA (Sw.) Nyl. Lich. Jap. 59, 1890. On bark: sterile. Mont Canala, June. "In moist forest, 1000 ft." 1303. Tropical Asia and America.

Var. MOLLIS Hue in Mém. Soc. Sci. Nat. Cherb. sér. 4, vii. 239, 1909. On decaying wood. Ignambi; in forest; 2000-4000 ft. 1743. Oceania (Java), Tropical America.

CROCYNIA sp. On branches. Riv. Ngoyé, May. "In *Spermolepis* forest on serpentine soil by river, 350 ft." 1097.

A sterile plant, forming small white subcontinuous scales on a dark hypothallus. Probably immature.

CROCYNIA sp. Riv. Ngoyé, 25th May. On bark. "In *Spermolepis* forest on serpentine soil by river, 350 ft." 1105.

A sterile form, consisting of small, crowded white scales on a dense brown hypothallus.

CROCYNIA CRUSTATA var. *MINOR* A. L. Sm.

The specimen, which is sterile, approaches very near to the description of *C. crustata* Hue, Sect. *Byssocaulon* (Mém. Soc. Nat. Cherb. sér. 4, vii. p. 243, 1909). It forms a continuous pale green glaucescent felt over very irregular bark, 8–10 cm. long and almost as wide. It is continuous, closely appressed, with a hyssoid white border and white below. Within, the tissues are as described by Hue, but of smaller dimensions, though the whole thallus is thicker. On bark. Mont Canala, June. "In moist forest, 1000 ft." 1299.

THELOTREMACÆÆ.

LEPTOTREMA ANDAMANICUM, comb. nov. (*Thelotrema andamanicum* Nyl. in Bull. Soc. Linn. Norm. sér. 2, vii. 1873, 168). On bark. Riv. Ngoyé. In *Spermolepis* forest on serpentine soil by river, 350 ft. May. 1099. S. Asia (I. of Andaman).

L. EPITRYPUM, comb. nov. (*Thelotrema epitrypum* Nyl. in Ann. Sci. Nat. sér. 4, xix. 1863, 334). 1107. From the same locality as the previous species. Tropical America (Cuba and New Grenada).

CÆNOGONIACEÆ.

CÆNOGONIUM LEPRIEURII Nyl. in Ann. Sci. Nat. sér. 4, xvi. 1862, 89. On Palm leaves. No number. Tropical countries.

CLADONIACEÆ.

THYSANOTHECIUM HYALINUM (Tayl.) Nyl. Syn. i. 186, 1860. On soil. Mont Koghi, April. "Whitish erect stalks, with pale brown apothecia. On bare serpentine soil: Niaouli-bracken formation, 1000 ft." 806. Tonghoué Mts., Jan. "Erect grey stalks, white disc-like apothecia, 500 ft." 179. Oceania (Australia, New Caledonia).

TH. HOOKERI Berk. & Mont. in Hook. Journ. Bot. v. 257, t. 10, 1846. "Plaine des Lacs. Common on ground sticks and leaves, 800 ft." 426. Oceania.

CLADONIA PYCNOCLADA (Gaudich.) Nyl. Lich. N. Zeal. in Journ. Linn. Soc. ix. 244, 1867. Baie Ngo, Feb. "Abundant on serpentine soil, in scrub formation, forming large white masses [also seen at Plaine des Lacs, Bogota, and elsewhere on serpentine]." 423. Australia, Asia, S. Africa, S. America.

CL. FLOERKEANA Sommerf. Suppl. Fl. Lapp. 128, 1826. On soil and old twigs. Tonghoué Mts., Jan. "Grey stalks tipped with bright crimson apothecia." 178. S. America, Europe.

CL. DIDYMA var. *MUSCIGENA* (Eschw.?, Nyl.) Wainio, Mon. Clad. Univ. i. 141, 1887. Tonghoué Mts., Jan. 178. Plaine des Lacs, 15th Feb.

"Common on ground, dead sticks, etc. Erect: red apothecia." 425. Mont Canala, June. "From bark of trees in moist forest, 1000 ft." 1302. Oceania, S. America.

CLADONIA AGGREGATA Ach. Lich. Suec. Prodr. 206, 1798. Baie Ngo, Feb. On ground among dead leaves, with *Cl. pygmaea*. 424. "On ground, dry scrub formation, serpentine." 717. Australia, New Zealand, India, S. Africa, S. America.

CL. RETEFORMA (Labill.) Fr. Nov. Sched. Crit. 21, 1826. On the ground. Plaine des Lacs, Feb. "Serpentine soil, very poor in humus." 422. Australia, Tasmania, New Zealand.

CL. VERTICILLATA (Hoffm.) Fl. Clad. 26, 1828. Mont Koghi, April. "On ground, 1000 ft., serpentine soil: Niaouli-bracken association." 770. Cosmopolitan.

STEREOCAULON RAMULOSUM Ach. Meth. 314, 1803. 1727. Australia, New Zealand, S. America.

LECIDEACEÆ.

LECIDEA (§ PSORA) FERRICOLA A. L. Sm., sp. nov.

Thallus albidus, continuus, grosse granulatus vel bullato-squamulosus, subeffiguratus. *Cortex* superior 45–50 μ lat. ex hyphis dense intricatis conglutinatis formata, gonidia protococcoidea, ca. 10 μ diam. stratum continuum ca. 40 μ lat. formantia; medulla ca. 150 μ lat. ex hyphis ca. 2–3 μ lat. intricatis constans. *Apothecia* nigra, nitida, 1–3 mm. lat., supra cristam thallinam nunc sparsa nunc crebre aggregata, convexa, interdum lobata, margine tenue, integro, parum elevato, intus granulis minutis inspersis; hypothecium nigrum, superne nigro-brunnea ex hyphis adscendentibus, conglutinatis constans; paraphyses tenues, non bene discretæ septatæ, sursum nigro-brunneæ, 70 μ alt.; asci clavati, 55–65 $\mu \times 15 \mu$; sporæ ellipsoideæ, hyalinæ, 12–14 $\mu \times 5$ –7 μ .

Ad saxum ferrugineum pulverescens. Mont Dore, May. On serpentine soil, 1000 ft. 847. *Thallus* and *apothecia* become powdered with iron dust from the substratum.

L. COMPTONII A. L. Sm., sp. nov.

Thallus tenuis, determinatus, stratum continuum formans, superficie minute plicatus vel granulatus, flavo-ochraceus. *Apothecia* prominentia, 0.5–1 mm. lat., novella disco plano flavo-ochraceo, margine integro nigro parum elevato cincta, deinde quasi morbosio-nigricantia; hypothecium rufo-brunneum; hymenium hyalinum ca. 80 μ alt.; paraphyses tenues arcuæ coherentes; asci oblongo-clavati; sporæ octonæ, ellipsoideæ, 12–15 $\mu \times 5$ –7 μ .

Ad lignum. 803.

The *thallus* forms a thin layer over the inequalities of the bark; it resembles somewhat an Australian species, *L. ludibunda* Müll.-Arg. (Lich. Beitr. n. 1162 in Flora, lxx. 321, 1887).

LECIDEA GONIOPHILA Schaer. Enum. Lich. 127, 1850. On rocks. Mont Montravel, N. of Nouméa. Europe, Japan, &c.

A very small specimen with a brownish-white subcontinuous thallus (K+ yellow) and minute brownish-black apothecia. The colourless hypothecium and the smaragdine tips of the paraphyses agree with those of the type, but the spores are on the whole smaller, measuring about $10-13 \mu \times 6 \mu$. It is associated with tufts of *Stigonema* sp.

MEGALOSPORA CASTANOCARPA A. L. Sm., sp. nov.

Thallus albido-glaucescens, continuus, sat lævigatus, tenuis, 60–80 μ cr. *Gonidia* protococcinea, ca. 7 μ diam. *Cortex* superior tenuis, decompositus, superne interdum hyphis superficie parallelis; cortex inferior sat crassus ex hyphis brunneis parallelis constans ad substratum arcte adhærens. *Apothecia* sessilia, turgido-convexa, castaneo-brunnea, 4–6 mm. lat., ca. 1 mm. alt., margine concolore mox evanescente; hypothecium albidum dense plectenchymaticum, gonidiis sparsis instructum; excipulum proprium ex hyphis radiantibus, conglutinatis, formatum; paraphyses arcte cohærentes, sursum flavescentes, tenues, ramosæ, apice paululum incrassatæ; asci longe clavati, ca. 200 $\mu \times 40 \mu$; sporæ saltem quarternæ, late ellipsoideæ, 1-sept. (membranes 5–7 μ crass.) 65–80 $\mu \times 22-32 \mu$.

Ad corticem arborum. Ignambi, 2000–4000 ft., Aug. 1738.

BIATORINA INTERMIXTA (Nyl.) comb. nov., var. *AGGREGATA* A. L. Sm., var. nov.

Thallus tenuis, cinerascens, minute granulatus. *Apothecia* parva, in acervulos sparsos aggregata, vel solitaria et tum usque ad 1 mm. lat.; hypothecium et epithecium rufo-brunnea, hydrate kalico color in violaceum sordidum mutatur; paraphyses conglutinatæ; sporæ rectæ vel leviter curvulæ, oblongo-ellipsoideæ vel fusiformes, 1-sept., 20–24 $\mu \times 3-4 \mu$.

Ad corticem arborum. Ignambi, 2000–4000 ft. Aug. 1746.

Differs from the species (New Caledonia) in the grouping of the apothecia, which are scattered over the thallus in button-like acervuli, and also in the somewhat narrower spores.

B. FUSCONIGRA A. L. Sm., sp. nov.

Thallus albido-glaucescens, crustaceus, effusus, minute isidio-squamulosus vel isidio-granulatus, sat tenuis. *Apothecia* parva, usque ad 0.8 mm. diam., rufo-brunnea, deinde nigra, interdum aggregata, margine tenue, integro, demum convexa margine excluso; hypothecium et epithecium rufo-brunnea, hymenio subconcolore; paraphyses graciles persistente conglutinatæ, apice non, vel leviter, clavato; sporæ octonæ, ellipsoideæ, hyalinæ, 1-sept., ca. 10–12 $\mu \times 2 \mu$.

Ad corticem arborum. Riv. Ngoyé. In *Spermolepis* forest on serpentine soil by river, 350 ft. May. 1100, 1106.

Distinguished by the minutely isidiose-squamulose thallus which follows the inequalities of the rugged bark, as well as by the apothecial characters.

BACIDIA CROCYNIOIDES A. L. Sm., sp. nov.

Thallus pallido-griseo-virens (K + flavus) plagas latas formans, squamulo-granulatus; granulae minutae, convexo-planae, sparse vel dense congregatae, interdum subimbricatae, ad substratum arcte coherentes, non corticatae, e hyphis ca. 4μ cr., membranis crassis, laminae minimo, crebre coalitis, compositae; gonidia protococcoidea, $5-8\mu$ diam., sparsa vel in glomeros aggregata. *Apothecia* sessilia, novella minuta concava, tum fere plana, marginata, solitaria vel congregata, interdum ad marginem apotheciorum vetustorum crescentia, ca. $.5-1$ mm. lat. margine pallide flexuoso. disco carneo tum ochraceo-flavo, intus albida; hypothecium e hyphis dense intricatis; perithecium e hyphis radiantibus compositum; paraphyses tenues, concretae, apice subclavatae; asci oblongo-clavati, ad basim paululum attenuati, $40\mu \times 7\mu$; spores aciculares, pluri-septatae, $25\mu \times 1-2\mu$.

Ad corticem arborum. Riv. Ngoyé. *Spermolepis* forest on serpentine soil by river, 350 ft., May. 1101.

Somewhat resembling *Crocynia* in the soft thallus and *C. gossypina* in the frequent "hen and chickens" arrangement of the apothecia. It is seated more or less on abundant brown fungus hyphae.

BUELLIA DISCIFORMIS var. *TRIPHAGMIA* (Nyl.) Boist. Nouv. Fl. Lich. pt. 2, 234, 1902 (*B. Lauri-Cassie* (Fée) Müll.-Arg.). On bark of *Ewotheca*. Baie Ouémo, Nouméa. Cosmopolitan.

B. STELLUTATA Mudd, Man. 216, 1861. On rocks; Mont Montravel, N. of Nouméa. Cosmopolitan.

B. GLAUCO-AREOLATA A. L. Sm., sp. nov.

Thallus crustaceus, nigro-determinatus, glauco-cinereus, minute areolatus, areolae ca. $.3$ mm. lat. planae vel subconvexae (K + flavus dein ferrugineus). *Apothecia* nigra, prominula, ca. 0.5 mm. diam., plana et marginata vel convexa; hypothecium brunneum, superne pallide flavescens; hymenium ca. $50-64\mu$ alt.; paraphyses tenues, clavato-capitatae, brunneo-pileatae; asci clavati, ca. $40\mu \times 10\mu$; spores octonae fuscae, 1-sept., ellipsoideae, $7-10\mu \times 4-5\mu$.

Ad saxa. Mont Montravel, Nouméa.

Distinguished by the bluish-grey thallus, by the rust-coloured reaction with potash, and by the apothecial characters. The paraphyses have a narrow brown cap like those of *Biatorina lenticularis*.

B. ALBIDO-FLAVA A. L. Sm., sp. nov.

Thallus crustaceus, laevis, granulato-areolatus, interdum nigro-determinatus, albido-flavus (K—), ca. 0.5 mm. cr. non corticatus, ad corticem arcte adherens; gonidia protococcoidea, $7-10\mu$ diam. *Apothecia* vulgo 1 mm. diam.,

vel latiora et lobulata, subimmersa, nigro-marginata, disco plano, olivaceo-viridi-pruinosa; hypothecium nigro-brunneum, crassum; hymenium usque ad $100\ \mu$ alt. fuscescens; paraphyses tenues, septatæ, apicibus parum incrassatis, ramosis; asci clavati, ca. $60\ \mu \times 15\ \mu$; sporæ ellipsoideæ aut fusiformes, fusæ, 1-septæ, $15-22\ \mu \times 7-10\ \mu$.

Ad corticem *Erothece*. Baie Ouémo, Nouméa.

The specimen is a very small one, but so distinctive that it has seemed worth while to give the diagnosis. In section, the epithecium is not coloured, though if the section be thick the pruina forms a dark line.

PHYLLOPSORA (Æ).

PHYLLOPSORA PARVIFOLIA (Pers.) Müll.-Arg. in Bull. Herb. Boiss. ii. App. 1, 45, 1894. On bark. Mont Koghi; stream-valley forest, 1000 ft., April. 802. Tropical countries, New Caledonia, &c.

EPHEBACEÆ.

THERMUTIS sp. A dense felt of the lichen but no fructification. On rocks, Mont Montravel, Nouméa.

COLLEMACEÆ.

LEPROCOLLEMA NOVA-CALEDONIANUM A. L. Sm., sp. nov.

Thallus crustaceus, tenuis, continuus, non corticatus, furfuraceus, fulvo-virescens. *Gonidia* nostocacea, e cellulis caeruleo-virescentibus $6-7\ \mu$ cr., glomeruloso-concatenatis, familias globosas formantia. *Apothecia* sessilia, $0.5-8\ \text{mm}$. lat., disco ochraceo, margine proprio pallidior, intus albida; hypothecium incolore vel flavum; paraphyses arcte coherentes, apice clavatæ, interdum ochraceæ; asci oblongo-clavati usque ad $60\ \mu \times 7\ \mu$; sporæ octonæ simplices, ellipsoideo-fusiformes, $10\ \mu \times 2-3\ \mu$.

Ad lignum vetustum. Mont Koghi; stream-valley forest, 1000 ft., April. 805.

The only other species, *L. americanum*, recorded by Wainio from Rio de Janeiro, differs in the form of the thallus and in the much larger spores.

SYNECHOBLASTUS BELENOPHORUS Müll.-Arg. Lich. Beitr. n. 166 in Flora, lxiii. 259, 1880. On bark. Nouméa (two specimens). Oceania.

S. NEMATOSPORUS A. L. Sm., sp. nov.

Thallus submonophyllus, irregulariter crispato-lobatus, virescens. *Gonidia* moniliformi-catenulata, ca. $5-6\ \mu \times 3\ \mu$. *Apothecia* immersa ca. $0.5-6\ \text{mm}$. lat., disco rufo-brunneo, margine thallino crasso, incurvo, integro; asci clavati, apice membranâ incrassato, ad basim attenuati, ca. $85\ \mu \times 12\ \mu$; sporæ aciculi-formæ, ca. $65\ \mu \times 2-2.5\ \mu$.

Plaine des Lacs. Gelatinous masses on trunks in valley forest, 1000 ft., Feb. 275.

The specimen was preserved in formalin, and when washed and dried it collapsed to an almost film-like expansion, somewhat wrinkled on the surface and dark brownish-green in colour. The spores were so closely adherent that it was difficult to note the septa.

LEPTOGIUM TREMELLOIDES Fr. Fl. Scan. 293, 1835. Ermitage stream; loose encrustation on bark, gelatinous dark brown; apothecia light brown. Jan. 231. Also on rocks; Mont Montravel, near Nouméa. Almost cosmopolitan.

Var. *AZUREUM* Nyl. Syn. i. 125, 1858. 1461. Cosmopolitan.

L. sp. (Sect. *Mallotium*). Sterile. Ignambi. On mosses in forest, 2000-4000 ft., Aug. 1739.

Thallus rather wide (about 10 cm.). A striking plant, dull cæruleo-brownish, beset with folioles and isidia; the under surface densely covered with short or long blackish hyphæ.

PANNARIACEÆ.

LEPIDOLEPTOGIUM A. L. Sm., gen. nov.

Thallus squamosus, adpressus vel adscendens, maxima parte gonidiis impletus; hypothallus niger, interdum bene evolutus; stratum corticale superius plectenchymaticum. *Gonidia* nostocacea, moniliformi-concatenata stratum medullare homœomericum, vel in parte inferiore gonidiorum destitutum; cortex inferior non bene evolutus. *Apothecia* parum elevata; excipulo thallino instructa; sporæ octonæ, simplices, incolores.

The above genus, owing to the cellular upper cortex, differs from *Lepidocollema* as *Leptogium* differs from *Collema*.

L. *MONTAGUEI* A. L. Sm., sp. nov.

Thallus squamulosus; squamulae laxè aggregatæ, adscendentes vel interdum adpressæ, lobulatæ, minute dactylino-diviæ vel angustè lacinulatæ, lacinia simplices vel irregulariter pinnatæ, lurido-griseæ, rhizidis nigricantibus, sparsis, substrato affixæ; hypothallus niger, dense intricatus. Thallus ca. 120 μ crassus; stratum corticale superius 15-20 μ cr. e cellulis duabus ad 10 μ diam. formatum; gonidia nostocacea, e cellulis glomeruloso-concatenatis, non aggregatis, composita, leviter violaceo-rubro tincta; stratum inferius e hyphis paucis, parallelis, formatum, hypothallus ex hyphis violaceo-nigris, ca. 5 μ cr. constans. *Apothecia* ca. 1 mm. lat. aurantiaca, plana, marginata, sæpe perforata vel soleæforme deformata, sparsa vel dense aggregata; margine thallino integro involuto; hymenium pallide brunneum, asci clavati ca. 60 μ \times 17 μ ; sporæ octonæ, late ellipsoideæ, 12-15 μ \times 7 μ .

Ad cortices. Riv. Ngoyé. In *Spermolepis* forest on serpentine soil by river, 350 ft., May. 1094.

Many of the apothecia are perforated or a side scooped out, thus presenting a horseshoe formation. A somewhat similar though less pronounced

deformation occurs in *Pannaria perfossa* Stirton, a New Zealand plant, but the apothecia of the latter have crenulate margins and smaller spores, and the structure of the thallus is different.

The specific name *Montaguei* commemorates the brilliant young zoologist, Paul Montague, with whom Mr. Compton was associated in the expedition to New Caledonia. Mr. Montague joined the army on his return to England and served in the R.F.C. He lost his life in an air-fight in Salonika.

LEPIDOLEPTOGIUM RUGULOSUM A. L. Sm., sp. nov.

Thallus squamulosus; squamulae variabiles adpresse vel plerumque adscendentes, spathulatæ ad apices sæpe immarginatæ, flabellatim rugulosæ, lurido griseæ, ad basim adfixæ ca. 1–2 mm. long., 1 mm. lat.; hypothallus niger, non bene evolutus. *Thallus* ca. 500 μ crassus; stratum corticale superius ca. 10 μ cr. monostromaticum; medulla ex hyphis intricatis et gonidiis nostocaceis cæruleo-virescentibus, rubentibusve, moniliformi-concatenatis; stratum corticale inferius tenue, indistinctum. *Apothecia* usque ad 1.5 mm. lat., disco aurantiaco, margine granulato; hypothecium citrinum, K + rubro-aurantiacum; paraphyses graciles, arcte coherentes; asci clavati, ca. 80 $\mu \times 16 \mu$; sporæ octonæ, ellipsoideæ, 12 $\mu \times 6 \mu$.

Ad corticem. Riv. Ngoyé. *Spermolepis* forest on serpentine soil by river, 350 ft., May. 1089.

PARMELIELLA FULVA A. L. Sm., sp. nov.

Thallus fulvo-aurantiacus, suborbicularis, laciniatus, ca. 5 cm. lat. versus centrum plus minus granulatus et areolatus. Laciniae arcte adnatæ, 3–4 mm. lat., stellato-radiantes, simplices vel divisæ, versus ambitum sensim dilatatæ, interdum crenatæ, subtus rhizinis nigris præditæ; supra leves vel irregulariter transverse rugosæ. Cortex superior plectenchymaticus, 25–30 μ lat. e cellulis ca. 12 μ lat. formatus; gonidia nostocacea, ca. 10 μ lat.; cortex inferior et rhizinae e hyphis nigro-brunneis formati. *Apothecia* convexo-plana, supra thallum parum elevata, ad centrum adfixa, ferrugineo-nigra, non marginata, sparsa vel aggregata, ca. 0.5–1 mm. lat. irregulariter orbicularia, subtus hyphis smaragdulis 5 μ lat. prædita; parathecium smaragdulum; hypothecium pallidum; hymenium 90–100 μ alt. incolor; paraphyses dense conglutinatæ, 3–4 μ lat. clavatæ; epithecium brunneo-vel smaragdulinigrum; asci clavati, ca. 45 $\mu \times 8$ –10 μ ; sporæ octonæ, hyalinæ, cymbæformes vel ellipsoideæ, bi-guttulatæ, simplices, 12 $\mu \times 3$ –4 μ .

Ad corticem. Cap Bocage. On bark of shrubs in serpentine scrub, 500 ft., July. 1463.

A very striking plant with an almost effigurate outline. The rugæ of the laciniae recall those of *Parmeliella plumbea*.

P. COMPTONII A. L. Sm., sp. nov.

Thallus squamulosus, lurido-griseus, corticatus, subtus albidus non-corticatus. *Squamulae* adscendentes, spathulatæ, ad basim late adfixæ usque ad

2 mm. alt. dense imbricatæ, crenatæ, vel in lacinias angustas sæpe minute pinnatas divisæ. Thallus ca. 175 μ cr.; cortex superior ca. 35 μ cr. e cellulis decompositis constans, lumen cellularum 7 μ diam. vel ca. 12 $\mu \times 7 \mu$; gonidia nostocacea 5 μ diam. stratum densum 50 μ lat. sub cortice formantia; hyphæ medullares, intricatæ 5 μ cr. stratum ca. 100 μ cr. formantes. Apothecia plano-convexa, rufo-brunnea, margine pallidiore cincta, sparsa vel in glomerulos parvos aggregata, irregulariter orbiculares, 0.3–1 mm. diam.; hypothecium flavo-brunneum; paraphyses ca. 2.5 μ cr. septatæ, arcte cohærentes; asci clavati, ca. 45 $\mu \times 8 \mu$; sporæ ellipsoideo-fusiformæ, hyalinæ, 7–8 $\mu \times 3$ –4 μ .

Ad lignum. Riv. Ngoyé. *Spermolepis* forest on serpentine soil by river, 350 ft. May. 1095.

The squamules are somewhat similar to those of *P. triptophylla* in colour, but rather lighter, much larger, and more densely imbricate.

PARMELIELLA sp. Thallus of spreading reddish-brown lacinia, irregularly crenate in outline, branched or simple, blunt at the tips, about 2–4 mm. wide, up to 12 mm. long, beneath densely pannose with dark hyphæ solitary or in strands, about 3 mm. long. Thallus about 140 μ thick, the upper cortex a layer of two cells with extremely gelatinous walls and restricted lumen; the gonidial zone narrow, of conglomerate blue-green algæ; the lower cortex of decomposed cells. Sterile. On bark. Mont Mou. Brown above, black filaments round edges and beneath. March. 713.

PANNARIA MARIANA Müll.-Arg. Lich. Beitr. n. 1159 in Flora, lxx. 321, 1887.

On trees. Ignambi. In forest, 2000–4000 ft. Aug. 1736. E. Indies, N. Caledonia, N. and S. America.

Var. **ISIDIOIDEA** Müll.-Arg. l. c.

Ermitage stream. "Encrusting stones by stream." Grey, fringed with black hairs." Jan. 230. Ignambi. In forest, 2000–4000 ft. Aug. 1736. E. Indies, New Caledonia, N. and S. America.

P. NIGROCINCTA (Mont.) Nyl. Syn. ii. 39, 1885.

On branches. Nouméa. Oceania, W. Africa, S. America.

PSOROMA SPHINCTRINUM (Mont.) Nyl. Syn. ii. 24, 1885. On wood. Ignambi. In forest, 2000–4000 ft. Aug. 1733, 1734. Africa, Oceania, S. America.

PS. ARANEOSA (Bab.) Nyl. Syn. ii. 23, 1885. On soil. Mont Humboldt. In moist gully forest, 1000 ft. May. 1086. Oceania (New Zealand).

PSOROMA sp. Thallus reddish-brown of small, mostly ascending, variously crenate-lacinulate squamules. Abortive apothecia alone present. On tree-trunks. Riv. Ngoyé. *Spermolepis* forest on serpentine soil by river, 350 ft. May. 1096.

COCCOCARPIA PELLITA Müll.-Arg., var. *PARMELIOIDES* Wainio, Lich. Brés. i. 209, 1890. On bark. Baie Ba. "On mangrove trunks and other trees by shore." 1462. Oceania (New Caledonia), N. and S. America.

Var. *CRONIA* Müll.-Arg. Lich. Beitr. n. 421 in Flora, lxx. 320, 1882. On rocks; Mont Montravel north of Noumea. N. and S. America.

STICTACEÆ.

LOBARIA INTERVERSANS, comb. nov. (*Ricasolia interversans* Nyl. in Flora, lxxix. 173, 1886). On bark. Mont Canala. In moist forest, 1000 ft. June. 1305, part. W. Africa.

LOBARIA sp. Mont Canala. In moist forest, 1000 ft. June. 1305, part. A sterile specimen, but with the same reaction as *L. interversans* (Med. K (CaCl) rose-red). The thallus is stouter and it may be *L. sublarvis*, which differs in having lobate margins to the apothecia, and narrower spores.

LOBARIA (§ *LOBARINA*) *SUBPINNATA* A. L. Sm., sp. nov.

Thallus foliaceus, glauco-flavescens vel pallide cervinus ca. 10–15 cm. lat. adscendens (?) non adpressus, versus ad basin laciniatus; laciniae sat angustatae, irregulariter et iterum subpinnatae, laciniae ultimae ad apicem saepe dilatatae et truncatae; pagina superior sorediis parvis, cinereo-albidis, adspersa; pagina inferior fere ad apicem pilis crebris fuscis instructa, ambitua subnuda (K—, (CaCl—). *Gonidia* nostocacea, caeruleo-virescentia, conglomerata, ca. 5 μ diam. *Strata* corticalia ca. 25 mm. lat. e seriebus cellularum formata; hyphis rhizoideis numerosis, connatis, usque ad 800 μ long. *Apothecia* non visa.

Ad ramulos arborum. Mont Arago. On bark of shrubs in serpentine scrub, 500 ft. July. 1466.

The lichen has a light graceful appearance unlike any other described *Lobaria*. The upper surface resembles that of *Sticta argyracea*. The under surface, at the tips of the laciniae, is occasionally golden-brown. The thallus is closely attached to the support where it touches, but the main part is free.

STICTA INTRICATA Del., var. *THOUARSII* Mudd, Man. 90, 1861. On bark. Mont Canala. "In moist forest, 1000 ft." June. 1298. Europe, S. Africa, Oceania.

S. CROCATA Ach. Lich. Univ. 447, 1810. On bark of tree. Baie Ouémo. 237. Co-mopolitan.

S. WEIGELII Wain. Lich. Brés. i. 189, 1890. On bark. Mont Canala. In moist forest, 1000 ft. June. 1301. Universal in tropical or subtropical regions.

STICTA DAMÆCORNIS Ach. Meth. Lich. 275, 1803. 1735. Tropical countries. Rare in Europe.

Var. *CANARIENSIS* Ach. Syn. Lich. 231, 1814. Mont Canala. Bark of trees in moist forest, 1000 ft. 1296. W. Africa, W. Indies, Brazil.

Lighter in colour than the species and with blunt-tipped laciniae.

S. VARIABILIS Ach. Lich. Univ. 455, 1810. Ignambi. "In forest, 2000-4000 ft." 1740. S. and E. Africa, Oceania.

S. HYPOSPILOIDES Nyl. Exp. Lich. N. Caled. 42, 1861. On bark. Large grey-surfaced, dichotomising thallus, drooping outwards from trunks. Valley forest, 600 ft. 715. Oceania.

S. COLENSOI Bab. ex Hook. Fl. N. Zeal. part 2, 274, 1855. On bark. Mont Canala, June. In moist forest, 1000 ft. 1300. N. Zealand, Tasmania.

S. AURATA Ach. Meth. Lich. p. 277, 1803. On dead branches, valley forest, 600 ft. 716. Mont Canala, June. In moist forest, 1000 ft. 1294. Cosmopolitan.

A second specimen is a deep rose-red, but differs from the similarly coloured *S. clathrata* De Not. and *S. aurora* De Not. in the presence of isidiose soredia on the margins of the laciniae.

Var. *PALLENS* Nyl. Syn. Lich. i. 361, 1860. On bark. Ignambi. In forest, 2000-4000 ft. August. 1731. New Zealand.

Distinguished by the paler colour and by the coating of short white hairs on the under surface and, more sparsely, on the upper surface.

S. DISSIMULATA Nyl. subsp. *MULTIFIDA* Nyl. Lich. N. Z. 37, 1888. On bark. Ignambi. In forest, 2000-4000 ft. 1742. New Zealand.

S. DEMUTABILIS Krempelh. form *LÆVIS* Krempelli. in Journ. Mus. Godeffroy, xiv. Heft 4, 6, 1873. On bark. Ignambi. In forest, 2000-4000 ft. 1729. Oceania (Samoa).

S. FREYCINETHI Del. Stict. 124, 1825. On branches. Grey surface, but yellowish, with black spots. 716. Valley forest, 600 ft. 740. Mont Canala, June. "In moist forest, 1000 ft." 1304. Oceania, Antarctica, S. America.

PERTUSARIACEÆ.

PERTUSARIA VELATA Nyl. Lich. Scand. 179, 1861. On bark of *Eurotheca*. Baie Ouémo, Nouméa. Cosmopolitan.

P. VELATOIDES A. L. Sm., sp. nov.

Thallus albidus, tenuis, minate rugulosus et sparse granulatus (K —, vel + obscure flavescens, K(CaCl) + rubens, CaCl —). Verrucæ fertiles numerosæ,

confertæ, ca. 0.5 mm. lat. vel minores, hemisphericæ, apice truncato, primo albide velato dein pallide carneo (CaCl + roseo-tincto), apothecium unum vulgo continentæ; sporæ solitariæ, ellipsoideæ, intus læves, ca. 135–150 μ long., 30–45 μ lat.

Corticola. Mont Arago, July. In damp forest, 1000 ft. 1466. Without locality. 1467.

Differs from *P. velata* Nyl. and from subsp. *subvelata* Nyl. in the negative reaction of the thallus with CaCl alone, in the absence of soredia, and in the smaller spores.

PERTUSARIA PYCNOTHELIA Nyl. Syn. Lich. Nov. Caled. 31, 1868. On bark of *Exothea*. Baie Ouémo, Nouméa.

P. LEIOPLACA Schaer. Lich. Helv. Spicil. 66, 1823. On bark of *Ficus*. Baie Ouémo, Nouméa. Cosmopolitan.

Var. OCTOSPORA Nyl. Lich. Scand. 182, 1861. On bark of *Exothea*. Baie Ouémo, Nouméa. Cosmopolitan.

The specimen shows a wrinkled areolate thallus, tinged greenish-yellow in places. The verrucæ are large and congregate. Spores measure 65–75 μ \times 30–35 μ .

P. CITRINA, A. L. Sm., sp. nov.

Thallus citrino-sulphureus, tenuis, minute areolatus vel purpuraceus, plerumque dense sorediatus (K—, CaCl + aurantiacus), soralia ca. 0.5 mm. lat.; verrucæ fertiles confertæ vel sparsæ, hemisphericæ, vulgo minutæ, 5–7 mm. lat., sed usque ad 1.5 mm. lat. CaCl + roseo-aurantiacæ. *Apothecia* solitaria vel plura: asci cylindricei; sporæ octonæ, ellipsoideæ, intus læves, ca. 65 μ long., 28 μ lat.

Ad saxa ferrugineo-arenosa. Mont Montravel, Nouméa.

Near to *P. sulphurea*, but persistently brighter in colour and differing in the form and colour of the apothecia, the discs of which in *P. sulphurea* take a violet colour with potash. The reactions of the thallus are also different.

LECANORACEÆ.

LECANORA SUBFUSCA var. CHLORONA Ach. Syn. Lich. 158, 1814. On bark of *Acacia*. Baie Ouémo, Nouméa. Cosmopolitan.

L. LUTESCENS (DC.) Nyl. Lich. Jap. 110, 1890. Baie Ouémo, Nouméa. Two specimens on *Ficus* bark; one on *Acacia* bark; one on *Exothea* bark. Oceania (Labuan), Japan, Europe.

L. GALACTINA subsp. DISPERSA Nyl. ex Cromb. in Grevillea, xviii. 68, 1890. On rocks. Mont Montravel, Nouméa. Cosmopolitan.

L. PARELLA Ach. Lich. Univ. 370, 1810. On bark of *Exothea*. Baie Ouémo, Nouméa. Cosmopolitan.

HÆMATOMMA PUNICEUM (Ach.) Wainio, Lich. Brés. i. 72, 1890. On bark of *Acacia*. Baie Ouémo, Nouméa. Frequent in the tropics.

H. BABINGTONII Massal. in Bull. Soc. Mosc. xxxvi. 260, pl. 2, 1863. On bark of *Acacia* and of *Exothea*. Baie Ouémo, Nouméa. Oceania.

PARMELIACEÆ.

HETERODEA MUELLERI (Hampe) Nyl. Syn. Lich. Nov. Caled. 9, 1868. The Monac, 11th Dec. On bare gritty earth on hillside: Niaouli association, 100 ft. Dec. 2388. Also from Nouméa. Oceania.

PARMELIA WAINII A. L. Sm., comb. nov. (*P. proboscidea* Wainio, Lich. Brés. i. 29, 1890). On bark. Canala. "Trunks near village: moist forest association, sea-level." 1471. S. Africa, S. America.

Described as *Parmelia proboscidea* Tayl. by Wainio and others in a misapprehension of Taylor's species. *P. crinita*, quoted as a synonym *pro parte*, is more nearly akin to *P. proboscidea*, and cannot therefore be used.

P. PERFORATA Ach. Meth. Lich. 217, 1803. On bark. Mont Canala. In moist forest, 1000 ft. June. 1306. New Zealand, Africa, S. America.

P. CRISTIFERA Tayl. in Hook. Journ. Bot. vi. 165, 1847. On bark. Canala. Trunks near village: moist forest association, sea-level. June. 1467, 1473. Asia, Oceania, S. America.

P. PERLATA Ach. Syn. i. 197, 1814. On rocks. Mont Montravel, Nouméa. Cosmopolitan.

P. TINCTORUM Despr. ex Nyl. in Bull. Soc. Linn. Norm. sér. 2, vi. 269, 1872. On bark. Mont Canala. In moist forest, 1000 ft. June. 1474. Canala: moist forest association, sea-level. 1295. Frequent in the Tropics.

P. CETRATA Ach. Syn. Lich. 198, 1814. On bark. Mont Canala. In moist forest, 1000 ft. June. 1732. Ignambi. "In forest, 2000-4000 ft." Aug. 1297. Cosmopolitan.

P. CONSPERSA Ach., var. *ISIDIATA* Leight. Lich. Fl. 135, 1871(?). On rocks. Mont Montravel, Nouméa. Oceania, Europe.

The specimen (sterile) agrees with *P. conspersa*, a cosmopolitan species, in habitat and in appearance, but the medulla is not stained with potash. The reaction medulla K(CaCl) + rose-coloured is the same as that of *P. acariospora* A. Zahlbr., a corticolous species from S. Brazil. In the absence of apothecia it is not possible to decide with certainty.

P. CIRCUMNODATA Nyl. in Journ. Linn. Soc., Bot. xx. 1884, 51(?). On bark. Cap Bocage. "Shrubs in serpentine scrub, 500 ft." 1465. East Indies (Penang)..

Nylander's specimen from Penang is sterile. The above, which is alike in thallus, bears numerous apothecia up to 2 mm. wide, the margins crenate when young but becoming subentire, the margin and under side beset with black setæ which tend to be less visible in the more developed fruits; the hypothecium is colourless; hymenium $50-60\ \mu$ high; asci clavate $40-50\ \mu \times 10-12\ \mu$; paraphyses concrete, the tips involved in reddish-brown mucilage; spores small, ovoid, or subglobose, $5\ \mu \times 7\ \mu$.

It would be necessary to secure fertile specimens from Penang to be quite sure of the specific identity of the specimen from New Caledonia. The black setæ, up to 1 mm. long, are a distinctive feature of the apothecia; they recall those of *Parmelia tiliacea* subsp. *carporhizans* (Tayl.) Nyl.

USNEACEÆ.

RAMALINA CALICARIS Fr. Lich. Eur. 30, 1831. On bark. Canala. "Trunks near village: moist forest association, sea-level." June. 1469. Cosmopolitan.

USNEA Plicata Web. in Wigg. Prim. Fl. Hols. 91, 1780. On bark. On living trunks in slight shelter, 600 ft. 719. Cosmopolitan.

U. LONGISSIMA Ach. Lich. Univ. 626, 1810. On bark. Mont Canala. In moist forest, 1000 ft. June. 1293. In tropical and subtropical countries; rare in Europe.

U. INTERCALARIS Krempelh. in Journ. Mus. Godeffroy, xiv. 4, 4, 1873. On bark. Canala. Trunks near village: moist forest association, sea-level. June. 1472. S. America, Oceania.

PHYSIACEÆ.

PLACODIUM GRISEO-VIRENS A. L. Sm., sp. nov.

Thallus uniformis, effusus, minute isidiosus, griseus vel pallide virens (K—). *Apothecia* 0.5 ad 2 mm. lat. sessilia vel thallo subimpressa, disco concavo ferrugineo-rubesciente, margine thallino crassiusculo, demum isidiosus, persistente: paraphyses sparse septatæ, ramosæ; asci oblongo-clavati, $55-65\ \mu \times 8-12\ \mu$; sporæ polariloculariæ, late ellipsoideæ, $15-17\ \mu \times 10\ \mu$.

Ad corticem arborum. Port Ngéa. Bark of *Ficus*. Jan. 236.

Distinguished by the isidiæ greyish-green thallus and by the rather large apothecia, the margins of which become in time smothered with isidia: these marginal isidia take a strong crimson stain with potash.

PL. (CALLOPISMA) CINNAMOMEUM, A. L. Sm., sp. nov.

Thallus cinereo-albidus, tenuis, areolatus, aut obsoletus (K—). *Apothecia* congregata sessilia, minuta, ca. 0.5 mm. lat., disco cinnamomeo, plano vel

convexiusculo (K + roseo), interdum tenue thallino-marginata; sporæ oblongo-ellipsoideæ, polariloculares, loculis parvis tubulo punctis, ca. $20\mu \times 6-7\mu$.

Ad corticem arborum. Baie Ouémo, Nouméa.

The species is distinguished by the whitish-grey thallus without parietin and by the rather narrow oblong spores. There are two specimens: one on *Ficus*, the other on *Acacia* (?).

PHYSICIA SPECIOSA (Wulf.) Fr. Lich. Eur. 80, 1831. Var. *HYPOLEUCA* Nyl. Syn. i. 417, 1860. On bark. Canala. "Trunks near village: moist forest association, sea-level." On rock. Mont Montravel, Nouméa. 1468. Cosmopolitan.

PH. ELÆINA (Wahlenb.) A. L. Sm. Monogr. i. 244, 1918 (*Ph. adglutinata* Nyl.). On bark of unknown tree. Baie Ouémo, Nouméa. Cosmopolitan.

PH. PICTA (Sw.) Nyl. Syn. i. 430, 1860. On bark. Canala. Trunks near village: moist forest association, sea-level. 1470. On bark of *Erotheca*. Baie Ouémo, Nouméa. On rock. Mont Montravel, Nouméa. Tropical and subtropical countries.

PYXINE MEISSNERI Tuckerm. Syn. N. Amer. Lich. 80, 1182. On bark of *Erotheca*. Baie Ouémo, Nouméa. Tropical countries.

Subsp. *CONNECTENS* Wainio, Lich. Brés. i. 154, 1890. Near Nouméa. On *Ficus* bark. 87. Brazil.

P. COCOES Nyl. Syn. Lich. ii. 2, 1885. Port Ngéa. On *Ficus* bark. Jan. 236.

Var. *SOREDIIATA* Tuckerm. in Proc. Amer. Acad. Arts & Sci. iv. 400, 1860. On *Ficus*. Port Ngéa. Jan. 236. Tropical countries.

P. RETIRUGELLA Nyl. in Ann. Sci. Nat. sér. 4, xi. 240, 1859. On bark of *Ficus*. Baie Ouémo, Nouméa. Polynesia, S. America.

RINODINA PELOLEUCOIDES A. L. Sm.

Thallus cinereo-albidus, sat tenuis, ca. 100μ cr., areolato-ramosus, lævis nigro-determinatus, K + flavens dein sanguineus; hypothallus niger. Gonidia usque ad 8μ diam.; hyphæ medullares interdum I + cæruleo-tinctæ. *Apothecia* fusco-nigra, parva (0.2-3 mm. lat.), margine thallino integro cincta; hypothecium rufo-brunneum; paraphyses graciles, conglutinatæ; epithecium fusco-nigrum; asci clavati, ca. $50\mu \times 10\mu$; sporæ fuscae, ellipsoideæ, 1-septatæ, ca. $12\mu \times 5\mu$.

Ad saxa (conglomerate rocks). Mont Montravel, Nouméa.

Differs from *Rinodina peloleuca* (Nyl.) Müll.-Arg. in the much smaller spores; like that species it recalls *Lecanora cinerea*, but is of a more minute and regular formation. The chemical reaction (not recorded in *R. peloleuca*) is very distinct.

FUNGI.

By ELSIE M. WAKEFIELD, F.L.S.

THE fungi of New Caledonia have not been very extensively collected. Previous lists have been made by Patouillard, who in 1887 enumerated 64 species which he found in the Museum at Paris, collected by Vieillard-Pancher. In 1902 a collection of 84 species was sent to Paris from the Museum at Nouméa, by Bernier, and between 1907 and 1911, various interesting species were collected by M. Le Rat, and recorded in the Bull. Soc. Myc. de France. In 1911-12, Sarasin and Roux made a large and fairly representative collection of fungi, and between 90 and 100 species were named at Kew. Descriptions of the new species included in this collection were issued in 1916 (*Vierteljahresschrift der Naturf. Ges. in Zürich*, Jahrg. 61), but owing to the war the full list was not published until 1920 (Sarasin & Roux, *Nova Caledonia, Botanik*, vol. i. d. ii.).

Prof. Compton's collection adds a number of new records, including two new species. It bears out the conclusion arrived at from the Sarasin and Roux collection, that the affinities of the fungus-flora are chiefly with that of the tropics of the Old World. There are, however, links with South America, and there is also a distinct temperate element.

In the following list, species marked with an asterisk (*) were included in the collection made by Sarasin and Roux. Those marked † have been previously recorded in literature from New Caledonia.

Of the 33 species here named, therefore, nine are new records for the island, two of them being apparently hitherto undescribed.

*† *SCHIZOPHYLLUM COMMUNE* Fr., Syst. Myc. i. 333. Ermitage Stream. Jan. 188. Cosmopolitan.

POLYPORUS DURUS Jungh. Præmissa in Flor. Crypt. Java, 1818, 62. Ignambi; 2000 ft. August. 1747. India, Malaya, Australia, Polynesia, Africa.

† *GANODERMA LUCIDUM* (Leys.) Karst. in Rev. Myc. 1881, No. 9, p. 17. Parasitic on coconut, and said to cause considerable loss. The single specimen included in the collection is the sessile form. Cosmopolitan. Previously recorded as a parasite on coconut in Ceylon. The symptoms of the disease described for Ceylon are similar to those observed in New Caledonia.

*† *G. AUSTRALE* (Fr.) Pat. in Bull. Soc. Myc. Fr. 1889, 71. Ermitage Stream. Feb. 427. Cosmopolitan in the tropics.

† *FOMES RIMOSUS* (Berk.) Fr., Nov. Symb. 66. Nouméa; common on old stumps and dying trees of *Acacia spirorbis*, woods of Port Despointes. 144.

India, Polynesia, Tropical Africa, Mascarene Islands, South Africa, North America, West Indies.

*† *POLYSTICTUS XANTHOPUS* Fr., Nov. Symb. 74. Ermitage Stream. Jan. 233. Mont Canala. June. 1354. Tropics of Old World.

*† *P. FLABELLIFORMIS* (Kl.) Fr., Symb. Myc. 74. Mont Canala. June. 1355. Ignambi; 2000 ft. August. 1748. In the gathering No. 1748, some of the larger specimens have an almost perfectly smooth, very dark-coloured, indistinctly zoned pileus. These agree exactly with Philippine specimens distributed under the name *P. microloma* Lév. *P. microloma* is probably only a form of *P. flabelliformis*. Tropics of Old World.

*† *P. SANGUINEUS* Fr., Nov. Symb. 75. "Common in the whole of the Nouméa district and elsewhere." 234. Cosmopolitan in tropical and sub-tropical regions.

* *LASCHIA CÆSPITOSA* Berk. in Journ. Linn. Soc., Bot. xiv. (1873) 58 (*Favolus cæspitosus* Berk. in *op. cit.* xiii. 167). Ermitage stream; on dead wood. Jan. 192. Ceylon, Malaya, Australia, Polynesia. Probably widely spread in the East.

The original description of this species was very scant and in some respects misleading. The present collection and gatherings made in 1911–12 in New Caledonia by Sarasin and Roux, all of which were preserved in fluid, show that when young and fresh the pileus is nearly always more or less pointed at the apex, sometimes even sharply umbonate. The same character is also seen in the original drawings of the Ceylon specimens (Thwaites, 182), which Berkeley referred as "*L. cæspitosa*, var." Older specimens may become more flattened, but there is usually a trace of an umbo. An amended description was given by Hennings in *Hedwigia*, xlii. 1903, p. 76, but his spore measurements are slightly too small. In all the specimens examined by me, including the type from Australia, the spores are broadly elliptical, or sometimes slightly pip-shaped, hyaline, $6-8 \times 4.5-5 \mu$.

Favolus albidus Masee differs only in the whitish pileus. *Polyporus mycenoides* Pat. from the description appears to be distinct. It is said to be phosphorescent, and this character has not been noted for any of the specimens of *L. cæspitosa* received at Kew.

*† *STEREUM CAPERATUM* (Berk. & Mont.) (*Thelephora lamellata* Berk. & Curt.). Ignambi; on dead logs in forest, 2000 ft. August. 1749. Malaya, Australia, Polynesia, South America, West Indies, Southern United States.

* *STEREUM RIMOSUM* Berk. in Hook. Journ. Bot. 1851, 169. Ermitage Stream; on dying tree. Jan. 155. The present specimens are very young, and more or less saucer-shaped, with the hymenium not yet cracked. The species is well marked in habit and possesses laticiferous ducts. When dry it is of a uniform fawn colour, but the collector's notes with this, and with a previous collection from the same island made by Sarasin, state that it is orange when fresh. In the present case it was also observed to exude a red juice when touched. India, Ceylon, Tropical Africa.

CORTICIUM CÆRULEUM (Schrad.) Fr., Epicr. 562. Locality not given. 720. Europe, North America, India, Ceylon, Malaya, Australia.

CLAVARIA FLABELLATA Wakefield, sp. nov.

Fungus albidus, magnus, ad 15 cm. altus, valde ramosus. *Rami* flabellato-divisi, compressi, læves, 1-5 mm. crassi. *Ramuli* suberecti, graciles, cylindracei, 1-1.5 mm. diam., apicibus fulvitinctis, sæpe flabellato-expansis. *Basidia* minuta, 10-15 \times 3 μ . *Spore* hyalinæ, ellipticæ, læves, 5-6.5 \times 3.5-5 μ .

Hab. Ad terram humosam in silvis. New Caledonia, Mont Canala; 1500 ft. 1276.

The species is readily distinguished by its large size and by the flattened branches. The fan-like expansions at the tips of the branchlets give it a very characteristic appearance. Preserved in formalin the plant is uniformly ochraceous or pallid, but when fresh it is white, with light brownish tips. It is said to be eaten by the natives.

C. STRICTA Pers. apud Fr., Syst. Myc. i. 468. Mont Canala; on rotting wood, damp forest; 1500 ft. June. 1179. Europe, North America. India, Ceylon (?).

C. FUSIFORMIS Sow. apud Fr., Syst. Myc. i. 480. Ignambi; on ground with little humus, in forest; 2000 ft. Aug. 1652. The basidia and spores are slightly smaller than in most British specimens, but otherwise the agreement is very close. Europe, North America, Ceylon (?), Madagascar.

* *AURICULARIA TREMELLOSA* (Fr.) Petch in Ann. Roy. Bot. Gard. Peradeniya, iv. 1910, 414. (cf. also Patouillard in Journ. de Bot. i. 1887, 226. Mont Dore. April. 710. Asia, Australia, Polynesia, Central and South America.

*† *HIRNEOLA POLYTRICHA* (Mont.) Fr., Fung. Natal, 146. Ermitage Stream. Jan. 218. Baie Ouémo; on dying branches of *Ficus* sp. Jan. 235. Cosmopolitan in tropical and subtropical regions.

*† *GUEPINIA SPATHULARIA* (Schw.) Fr., Elench. ii. 32. Mont Mou. March. 706. Probably cosmopolitan in tropical, subtropical, and warm temperate regions.

†CLAVARIOPSIS PULCHELLA Pat. & Har. in Bull. Soc. Myc. Fr. xxviii. 1912, 280. Mont Koghi; 1000 ft. April. 797.

No spores are present on these specimens, which are preserved in formalin, but the macroscopic characters agree with those described for *C. pulchella*.

Only recorded from New Caledonia.

CLAVARIOPSIS sp. Ignambi; 1500 ft. Aug. 1683.

Although the specimens are not in sufficiently good condition for determination, it seems worth while putting the occurrence on record, as so few species of this genus are known. The plants are caespitose, 2-3 cm. high, and more or less dichotomously branched, usually in one plane so as to form flattened expansions. The substance is very firm, and the colour when fresh dingy yellowish-white. Possibly the species is *C. pinguis* Holterm., but no spores are present, and it has not been possible to trace the varying forms of basidia described by Holtermann.

*†DICTYOPHORA INDUSIATA (Pers.) Fischer in Sarasin & Roux. Nova Caledonia, i. pt. i. 1914, 3. Mont Mou; on the ground, in old burnt-out Lantana area. March. 586. Cosmopolitan in the tropics.

†LERATIA SIMILIS Pat. in Bull. Soc. Myc. Fr. xxiii. 1907, 52. Ignambi; on dead wood in forest; 3500 ft. Aug. 1628.

In these specimens the columella is not limited to the base of the fruit-body as Patouillard figures it. It tapers gradually upwards, and passes imperceptibly into the gleba near the upper surface. The cavities of the gleba are small, hence the head is rather firm to the touch. The colour of the peridium when fresh is described as "light scarlet." Spores $12-15 \times 6-9 \mu$.

Only known from New Caledonia.

*†LERATIA SMARAGDINA Pat. in Bull. Soc. Myc. Fr. xxv. 1909, 33. Ermitage Stream. Jan. 190. Mont Mou. March. 709. Tonine; 2000 ft. Sept. 1952.

On dead logs in forest. These specimens also show a columella of varying development. In one case it reaches to the top of the fruit-body, and is continuous with the peridium as in *Secotium*. All the specimens being young, the mode of dehiscence is not evident, and it has not been possible to ascertain the relationship between this genus and *Secotium*.

The colour appears to vary in the fresh state, for while the formalin specimens do not differ from one another in microscopic details, the collector's notes give No. 190 as "peacock-blue," No. 709 "dull green," and No. 1952 "dark blue."

*†LYCOPERDON GEMMATUM (Batsch.) Fr., Syst. Myc. iii. 36. Ignambi; 1500 ft. Aug. 1685[i]. Specimens very young. Cosmopolitan.

†*ÆCIDIUM BALANSÆ* Cornu ex Patouillard in Bull. Soc. Myc. Fr. 1887, 173. Ignambi; 3500 ft.; on leaves of *Agathis* sp. and occasionally on the young shoots, causing slight hypertrophy. July. 1551. Malaya, Polynesia.

†*XYLARIA POLYMORPHA* (Pers.) Grev., Flor. Edin. 35. Mont. Canala; 3000 ft. June. 1213. Cosmopolitan.

X. ANISOPLEURA Mont. Syll. Crypt. 204, n. 688. Mont Mou. March. 707. Ceylon, Tropical Africa, West Indies, South America.

†*X. INVOLUTA* Kl. ex Cooke in Grevillea, xi. 1883, p. 82. For synonymy see Bres., Ann. Myc. v. 1907, pp. 240–241. Mont Canala; 2000 ft. June. 1212. Ignambi; 3500 ft. Aug. 1591.

The specimens are very fine, and being preserved in formalin they have retained their natural size and shape, so that the appearance is very different from that of dried specimens.

Probably cosmopolitan in the tropics.

X. FLABELLIFORMIS (Schw.) Berk. & Curt. in Journ. Linn. Soc., Bot. x. (1868) 1869, 381. Ermitage Stream. Jan. 189. Ceylon, Malaya, Australia, Tropical Africa.

HYPOXYLON ANNULATUM (Schw.) Mont. in Gay, Hist. de Chile, vii. 1850, 445. Ermitage Stream. Jan. 217. Abundant. Malaya, Australia, New Zealand, Tropical Africa, South America, West Indies, Southern United States.

**KRETZSCHMARIA CENOPUS* (Fr.) Sacc. Syll. i. 388. Ermitage Stream. Very common. Jan. 219. Ceylon, Malaya, Tropical Africa, West Indies, South America.

†*DALDINIA VERNICOSA* (Schw.) Cos. & De Not. in Comm. Soc. Critt. It. i. pt. 4, 1863, 198. Mont Dore; on dead branches of *Casuarina*; 1000 ft. April. 685.

The species differs from *D. concentrica* in the soft, whitish zones, separated by dark lines. Spores $13-15 \times 7-9 \mu$.

Europe, India, West Indies, North America.

†*D. ESCHSCHOLZII* (Ehrenb.) Rehm in Ann. Myc. ii. 1904, 175. (*D. concentrica* var. *microspora* (Starb.) Theissen; *D. vernicosa* var. *microspora* Starb.; probably *D. cognata* Har. & Pat.) Paompai; 100 ft. Sept. 1915.

Theissen considers this merely as a variety of *D. concentrica*. The constant association of small spores with the conspicuous coppery or purplish incrustation, however, appears to the author to be a distinction sufficient to merit specific rank. The species varies from completely sessile to more or less

distinctly stipitate forms, and occasionally, as in the present specimen and in *D. cognata*, several stromata become fused together. Spores $8.5-10 \times 4-5.5 \mu$. Polynesia, Tropical Africa, South America.

MEGALONECTRIA PSEUDOTRICHIA Speg. in Fung. Arg. Pug. iv. 1880, 82. Locality not given. Common in the tropics.

ANTENNARIA PANNOSA Berk. in Hook. Lond. Journ. Bot. ii. (1843), 640. Kuakué. May. 954. Frequent in the scrub area on various trees; often associated with scale insects and bark-living larvæ.

The species is distinguished from *A. Robinsonii* by the stouter hyphæ, and by the moniliform threads being slightly rough (punctate). Compared with *A. scoriadea*, the hyphæ are more frequently branched, and the branches are more slender towards the apex; moreover, there is greater variety in the types of hyphæ present. No form of fruit-body is present in these specimens. South America.

EXOASCUS CORNU-CERVI Sadeb., Die parasitische Exoascaceen, 68 (*Taphrina cornu-cervi* Giesenh.). Mont Mou; on fronds of *Aspidium aristatum*. March. 705.

The peculiar forked outgrowths were noted to be white when fresh, but in formalin, as in all the dried material seen, they have become quite black.

Distribution probably that of the host. Recorded from Nepal, Ceylon, Fiji, Samoa, Queensland. In the Kew Herbarium there is a previous specimen from New Caledonia on a collection of *A. aristatum* Sw., made by Deplanche.

ENCÆLIA NEO-CALEDONICA Wakefield, sp. nov.

Ascomata breviter stipitata, cæspitosa, coriacea, ad 14 mm. diam., sæpius contorta, extus ferruginea, minute tessellato-verrucosa. *Discus* fuliginosus, applanatus vel undulatus, margine involuto cinctus. *Asci* clavati, in stipitem passim attenuati, $110-120 \times 5-6 \mu$, octospori. *Spore* monostichæ, ellipticæ, hyalinæ, $9-11 \times 3.5-4 \mu$. *Paraphyses* ascos superantes, sursum brunneæ, clavato-incrassatæ, 3.4μ diam., deorsum hyalinæ, filiformes.

Hab. Ad truncos emortuos, in silvis, New Caledonia. Oct. 2194.

A large and distinct species, differing from *E. furfuracea* in the spores and in the nature of the outer covering. The latter consists of minute, closely-set pyramidal or conical warts, which are made up of chains of oblong or polygonal bright brown cells, $8-10 \mu$ in diameter.

MYCETOZOA.

By G. LISTER, F.L.S.

THE collection contains ten species. They were found in the high forest within thirty miles of Nouméa, and were all on dead wood except one which was on dead leaves. It is curious that prolonged search in these undisturbed tropical woods should not have resulted in a larger number of species being obtained. Possibly the climate was too wet for their perfect development. Mr. Compton describes the forests remaining moist for long periods; the plasmodia seemed rarely to form sporangia, and the latter soon became a prey to mould. He writes:—"Rotting logs lying across streams appear to be the most productive spots; once I found four species on a single log, but all unrepresentable things." In spite of these adverse circumstances the specimens collected are in beautiful condition; they were preserved in an air-tight box, to the cork lining of which they were firmly fastened by pins.

The following is a list of the species with notes on their characters and distribution:—

PHYSARUM VIRIDE (Bull.) Pers., var. *AURANTIUM* Lister. A large development on dead wood; the small hemispherical sporangia are on long, slender, pale stalks. This variety with orange-yellow sporangium-walls is far less common than the typical lemon-yellow form.

Distribution. Europe, including the British Isles, South Nigeria, Borneo, New Zealand, Japan, North and South America.

P. ROSEUM Berk. & Broome. A group of typical crimson sporangia with orange-brown stalks was found on dead wood.

Distribution. Not common. South Nigeria, Ceylon, Java, Borneo, South Japan.

DIDYMIUM NIGRIPES Fries. On dead leaves. This is the usual form with dark brown stalks and columellæ.

Distribution. Abundant in temperate and tropical regions.

STEMONITIS SPLENDENS Rost. A forest of sporangia 22 mm. high was found on dead wood covering an area of several square inches. The surface net of the capillitium shows an approach to that of *S. herbatica* Peck in having rather angular and spinose meshes from 15–30 μ in diameter. Found abundantly growing on tree-trunks a few feet above the ground.

Distribution. Abundant in the tropics and in the United States of America; less common in Europe.

S. FERRUGINEA Ehrenb., var. *VIOLACEA* Meylan, *in litt.* This specimen consists of small scattered clusters of violet-brown sporangia, 5–6 mm. high,

on dead wood. The surface net of the capillitium has rather small, very uneven meshes bounded by slender threads; the spores are minutely spinulose, 5–6 μ diam., with reddish-lilac rather firm walls. This is a puzzling specimen, holding a position intermediate between *S. ferruginea* and *S. pallida* Wing. With the former it agrees in the small size of the spores, and with *S. pallida* in the scattered habit of the sporangia and the uneven surface net of the capillitium; the spores are browner than in typical *S. ferruginea* and less grey than in *S. pallida*. M. Meylan finds a similar form with more closely clustered sporangia in the Jura mountains, which he has called in his letters *S. ferruginea* var. *violacea*, a name that may be adopted for convenience of reference. In this variable genus it appears that almost endless forms may be met with connecting the described species; *S. fusca* Roth., however, is always distinguishable by the reticulated markings of the spores.

Distribution. Typical *S. ferruginea* occurs in temperate and tropical regions, but is perhaps especially abundant in warm climates.

COMATRICHA TYPHOIDES (Bull.) Rost. A large growth was found on rotten wood, typical except that the silvery membranous sheath which usually clothes the whole stalk is confined to the upper third in these sporangia.

Distribution. Common in temperate and tropical regions.

DICTYDLETHALIUM PLUMBEUM (Schum.) Rost., var. ENTHOXANTHUM (Berk.) G. Lister, var. nov. *Æthalia* 2–3 mm. thick, with bright yellow spores. The present specimens consist of large greenish-yellow *æthalia* 50–60 mm. diam., 1.7–2 mm. thick, surrounded by a white membranous hypothallus; the dome-like apices or caps of the component sporangia are convex and minute, measuring 40–60 μ diam.; the threads connecting them with the basal membrane are winged and broad, 7–9 μ diam. This robust variety was first found in Sikkim, and named by Berkeley, *Reticularia entoxantha* (Hook. Journ. Bot. iii. p. 201, 1851); Mr. Petch has since collected it in Ceylon. A link connecting it with the widely distributed typical form was found by Prof. Thaxter in Chili; this consists of large *æthalia* 2 mm. thick having the usual clay-coloured spores.

LYCOGALA EPIDENDRUM (L.) Fries. Specimens of both the typical form and var. *tessellatum* Lister were obtained; the latter have dark brown *æthalia*, 3–6.5 mm. diam., rough with the characteristic many-chambered vesicles.

Distribution. The typical form is abundant in temperate and tropical regions; var. *tessellatum* is much rarer, and has been obtained in the Cameroons, West Africa, Ceylon, Java, New Zealand, Texas, Philadelphia, and the State of New York.

ARCYRIA DENUDATA (L.) Sheldon. Four specimens were found ; three are of the usual crimson colour ; the fourth is unusual in having almost scarlet sporangia, the capillitium, however, is typical.

Distribution. Abundant in temperate and tropical regions.

A. CINEREA (Bull.) Pers. A few clusters of pale drab sporangia with typical papillose capillitium were found on dead wood.

Distribution. Common in temperate and tropical regions.

This interesting collection confirms on the whole the remarkable constancy of the specific characters of the Mycetozoa, and gives a further proof of the wide distribution of many of the species. A large number of Mycetozoa appear to thrive equally well in warm or cool climates, but certain species may be considered especially characteristic of warmer regions. As examples of these in the present collection, *Physarum roseum* and *Stemonites splendens* may be mentioned ; on the other hand one notes the absence of any species of *Trichia*, a genus abundantly represented in temperate woods, but comparatively rare in the tropics.

On Charophyta collected by Mr. Thomas Bates Blow, F.L.S., in Ceylon.

By JAMES GROVES, F.L.S.

[Read 3rd November, 1921.]

(PLATE 6.)

IN the course of travels in various parts of the world, extending over many years, Mr. Blow has collected a very large number of specimens of Charophyta, which he kindly handed over to my late brother and myself.

The countries in which the collections were made are:—West Indies (1895); Ceylon (1895 & 1898); Western Australia (1895–6); South Australia (1896); New South Wales (1896); Victoria (1896); Northern Territory (1896); New Zealand (1896); Straits Settlements (1896); Tunis (1897); Japan (1896–9); India (1899 & 1908); Spain (1914); France (1920–1); Portugal (1921).

Although often collecting and preserving the plants under difficult conditions, Mr. Blow has maintained a high standard of excellence in his specimens, and it has been a great pleasure to have such exceptionally good material to deal with.

The specimens collected in the West Indies formed the subject of a paper which was read before the Society on the 16th of December, 1897, which appeared in its Journal, Botany, xxxiii. pp. 323–6 (1898).

My late brother determined a considerable number of the specimens from the other gatherings, but we were unable in his lifetime to report completely on any of them.

The present paper deals with the two collections from Ceylon, by far the most extensive which have been made in that island.

The first collection was made in the course of journeys along the west coast and in the high ground in the central parts of the island, in November 1895, when some of the plants were immature; the second on the south coast, in January 1898, when most of them had well-developed fruit.

In many cases the specimens were collected in the disused tanks, some of them like small lakes, which formed part of the extensive system of irrigation in existence many centuries ago, but now abandoned.

A complete set of specimens is in my own herbarium, which will ultimately be handed over to the British Museum. Where there are duplicates they will be distributed to Kew and other public herbaria.

NITELLA ACUMINATA, Braun in Hooker's Journ. Bot. i. (1849) p. 292 (as var. *Bellangeri*).

Dambool, Central Province, 6th Nov. 1895, no. 6; Anuradhapura, LINN. JOURN.—BOTANY, VOL. XLVI.

N. Centr. Prov., 7th Nov. 1895, no. 7; Tirupane, N. Centr. Prov., 9th Nov. 1895, no. 8; Negumbo, Western Prov. (at sea-level), 15th Nov. 1895, no. 9; Tangalla (shallow tank), Southern Prov., 8th Jan. 1898, no. 30; near Dikwella (roadside stream), South Prov., 9th Jan. 1898, no. 31.

Slightly differing forms of this widely-distributed extra-European species. The comparative length of the primary rays and dactyls is extremely variable, even in specimens of the same gathering. This is particularly noticeable in the Anuradhapura plant, the sterile branchlets on some examples of which have the extremely short dactyls of the var. *Bellangeri* (the type of Braun's species), while in others the dactyls are half the length of the primary rays; in the Tirupane plant the dactyls are in some cases nearly as long as the primary rays. The character would therefore seem to be of little value in this species. The Dikwella plant is of more flexible habit than the others, due no doubt to the habitat. Oospores measured c. $275\text{--}310\ \mu$ long, c. $250\text{--}275\ \mu$ broad, c. $175\text{--}225\ \mu$ thick, antheridia c. $275\ \mu$ in diameter. Oogonia often clustered. This species was previously collected by Trimen at Galle about 1881.

N. acuminata differs from *N. flexilis*, Agardh, and *N. laxa*, Allen, in the much smaller antheridia and oogonia, the spiral-cells of the latter not swelling at the apex, in the persistent coronula and in the decoration of the oospore-membrane, and from the first-named in the conspicuously tapering dactyls with long, sharp points.

NITELLA MUCRONATA, Miquel in van Hall, Fl. Belg. sept. ii, p. 428 (1840) *sens. lat.*

Botanic Gardens, Peradeniya, Centr. Prov., Nov. 1895, no. 10.

A single specimen without ripe fruit, which I can only refer to this species in a broad sense until further specimens are forthcoming. The dactyls have the characteristic proportionally narrow apical cells, and are sometimes 3-celled. The branchlets are 2-3 times forked, gametangia being produced at each furcation. The antheridia attain to c. $325\ \mu$ in diameter. A sterile plant from Anuradhapura collected 7th Nov. 1895, No. 24, probably also belongs to this species. A form of *N. mucronata* was previously collected in Ceylon by Ferguson.

N. PSEUDO-FLABELLATA, Braun in Braun & Nordstedt, Fragm. Monogr. Charac. (1882) pp. 12 & 54?

Newera Eliya (at c. 1980 m.), Centr. Prov., Nov. 1895, no. 11.

Apparently a form of this variable species, or group of species, having the branchlets 2-3 times forked, the primary rays of variable length, but sometimes more than half as long as the entire branchlet, the secondary rays 5-6, the tertiary 4-5, of which usually one only is again divided into 3-4

quaternary rays. The dactyls are usually rather long and are uniformly 2-celled, the penultimate cell acuminate truncate, the ultimate cell very sharp-pointed, c. $110\ \mu$ long, $40\ \mu$ broad at base. The first furcation of the branchlets sterile with a central ray; gametangia produced at the second and often at the third furcation. Oogonia c. $400\ \mu$ long (excl. coronula), $300\ \mu$ broad; coronula c. $33\ \mu$ high, $50\ \mu$ broad. Oospore golden to dark brown, c. $250\ \mu$ long, $225\ \mu$ broad, $150\ \mu$ thick, with 7–8 fine, well-marked but not flanged ridges; membrane imperfectly reticulate with about 6 large meshes between the ridges. Antheridium c. 250 – $275\ \mu$ in diameter. •

A curious point of nomenclature arises in connexion with this species. Braun first published the name *N. pseudo-flabellata* in 1866, in 'Die Preussische Expedition Ost-Asien,' p. 143, but without any description, and I cannot find that the species was described until 1882 (in Braun & Nordstedt's 'Fragmente.' In the meanwhile Dr. Nordstedt in 1880 (Act. Univ. Lund, xvi. iv. p. 16) described a *forma mucosa* of *N. pseudo-flabellata* (sec p. 100). Some strict nomenclaturists may contend that, being the first described the *forma mucosa* is the type of the species, although it is quite clear that it was Nordstedt's intention when describing it to differentiate it from what he regarded as the type, i. e. a plant without mucus surrounding the fertile heads.

Dr. Nordstedt describes the oospore-membrane of the Chinese and Javanese *N. pseudo-flabellata* as "etwas schwammig." Dr. Allen refers to that of the former as felted, but includes as varieties of the species one plant having the oospore-membrane faintly granulate and another having it perfectly smooth. If, as seems probable, the decoration of the membrane is a reliable character, it may be necessary to separate this into several species.

NITELLA LEPTODACTYLA, sp. nov. (Pl. 6.)

Section (Braun & Nordstedt):—Diarthrodactylæ, homœophyllæ, monoicæ, macrodactylæ, flabellatæ, gymnocarpæ.

Monœcia. Caulis tenuis, diametro, c. $275\ \mu$; internodia ramulorum longitudinem bis-quinquies superantes. Verticilli homomorphi, diametro c. 18–25 mm. Ramuli 6–7, 2–4-furcati, longitudine radiorum gradatim minuenta; radius primarius c. $150\ \mu$ crassus, ramuli totam longitudinem dimidio æquans vel superans; radii secundarii vulgo 7; tertiarii 4–5, quorum vulgo nonnulli simplices sunt; quaternarii 3–5; interdum quaternarii nonnulli denuo furcati, radibus quinaribus 3–5. Dactyli ramulorum plene evolutorum valde elongati recti plus minusve rigidi, semper 2-cellulati; cellula inferior, pæne totam longitudinem crassitudine æquabile, extremitate distale rotundata leviter fastigata; cellula ultima anguste conica, longitudine ($\rightarrow 90\ \mu$) diametrum ad basem sæpe quinquies superante, versis apicem acutum fastigata.

Oogonia et antheridia ad furcationes secundæ tertiæ et quartæ (haud ad

primæ) prolata, sæpe conjuncta. Oogonia solitaria, ovoideo-ellipsoidea, long. (coronula exclusa) c. $325\ \mu$, lat. c. $265\ \mu$; coronula alt. c. $30\ \mu$, lat. $60\ \mu$, persistens. Oospora subrotunda rubro-brunnea atra, long. $225\text{--}230\ \mu$, lat. $200\text{--}220\ \mu$, crass. c. $125\ \mu$, liras humiles sed conspicuas 7–8 exhibens, non cristata; membrana subtiliter et hebetè granulata. Antheridia diametro c. $225\ \mu$.

Moratuwa, between Colombo and Galle, West. Prov., Nov. 1895, no. 12.

A slender, graceful plant, probably attaining a height of about 30 cm., with long internodes, resembling in habit an extended form of *N. gracilis*, but with firmer rays, the dactyls uniformly 2-celled, straight and rigid, resembling those of *N. tenuissima*. I have not seen a specimen of *N. gracillima*, Allen, but from the author's description and plate, *N. leptodactyla* would appear to resemble it in habit and in the long cylindrical dactyls, but to differ in the size of the fruit, the character of the ridges on the oospore, and the decoration of its membrane. It differs from *N. mucronata* and the near allies of that species in habit, the number of secondary and tertiary rays, the sterile first node, the size of oospore, &c., and from that species and *N. pseudo-flabellata* in the comparative length and tenuity of its dactyls and the decoration of the oospore-membrane. The uniform length of the dactyls as well as their tenuity distinguish it from the subbrachydactylous series, which includes *N. oligospira*, *N. orientalis*, and *N. expansa*.

NITELLA MUCOSA, sp. nov. *N. pseudo-flabellata*, Braun, forma *mucosa*, Nordst. in Act. Univ. Lund, xvi. iv. (1880) p. 16.

Panadura (at sea-level), West. Prov., 16th Nov. 1895, no. 14; Moratuwa, Nov. 1895, no. 13; shallow tank, Tangalla, 8th Jan. 1898, no. 32; Dikwella, 9th Jan. 1898, no. 33; Amblangoda, South Prov., 12th Jan. 1898, no. 34.

Resembling *N. pseudo-flabellata* in the proportionate length of the primary ray and in the number of tertiary rays, but differing from that species in having the fruiting whorls enveloped in thick mucus and from the typical forms thereof at least in the granulate oospore-membrane. The size of the oogonium and oospore is variable. In the description of the type plants collected by Dr. Berggren in New Zealand the dimensions of the latter are given as, length $300\text{--}320\ \mu$, breadth $285\text{--}300\ \mu$. In the more robust plant collected by Cheesman, also from New Zealand, the oospores are about $350\ \mu$ long, $325\ \mu$ broad. The oospores of the Ceylon plants measured, except no. 13, range from $250\text{--}300\ \mu$ long, $225\text{--}250\ \mu$ broad, while those of no. 13 are only about $200\ \mu$ long and $175\ \mu$ broad.

N. OLIGOSPIRA, Braun in Monatsb. Akad. Berl. 1858, p. 357.

Dambool, Nov. 1895, nos. 15 & 16; Tirupane, 8th & 9th Nov. 1895, no. 17; shallow tank, Tangalla, 8th Jan. 1898, nos. 35 & 36.

This variable and rather indeterminate species seems to occupy an intermediate position between the sections *Macrodactylæ* and *Brachydactylæ*.

The dactyls are of very unequal length on different branchlets and the ultimate furcation is often fertile. In the Ceylon plants the sterile ultimate furcations with decidedly shortened dactyls are by no means frequent. The branchlets are 2-3, occasionally 4 times furcate. The plants resemble *N. gracilis* in habit, but the dactyls are uniformly 2-celled, and the ripe oospores (often lacking) have the characteristic netted membrane.

NITELLA MICROCARPA, Braun in Monatsb. Akad. Berl. 1858, p. 357.

Roadside stream near Dikwella, 9th Jan. 1898, no. 37.

A large rather robust plant, the branchlets about 3 cm. long. The abbreviated dactyls characteristic of the section are by no means numerous, the greater number being fairly long and proceeding from fertile nodes. The oogonia are clustered. The oospores, which are golden-brown, are about $250\ \mu$ long, $215\ \mu$ broad, and show about 6 fine well-marked ridges; the membrane has a very regular finely reticulate decoration. In Braun's original description of the species, founded on plants collected by Weigelt at Paramaribo, Dutch Guiana, and by Duchassaing near Panama, the length of the oospore is given as .18 mm. We have not seen the former, but on a specimen of the latter we have measured oospores exceeding $250\ \mu$ in length.

Apparently not previously found in Ceylon.

N. ROXBURGHII, Braun in Hooker's Journ. Bot. i. (1849) p. 293.

Tirupane, 9th Nov. 1895 (immature), nos. 18 & 19; Negumbo, 13th Nov. 1895, no. 20; Tangalla, 8th Jan. 1898, nos. 38 & 39, the latter from a shallow tank.

These specimens represent a large robust plant with somewhat the habit of *Tolypella intricata*, but with laxer fruiting heads; the sterile branchlets, which attain to a length of 4 cm., are sometimes only twice furcate, the rays divaricate. The plant from Tangalla, no. 39, has good ripe fruit; the oospore is of a dusky yellow-brown, is nearly round (length c. $250\text{--}275\ \mu$, breadth c. $240\text{--}275\ \mu$), and shows about 6 strong ridges. The membranes of this and the Negumbo plant have a fine coral-like netted decoration. Sterile specimens from jungle-pool, near Kandy, Centr. Prov., 5th Nov. 1895, no. 21, and Maradankadawile, N. Centr. Prov., 6th Nov. 1895, no. 22, both probably belong to this species. The former is a smaller form than any of the others, with much shorter branchlets and very divaricate rays.

Apparently not previously found in Ceylon.

NITELLA sp. (statu immaturo).

Section (Braun & Nordstedt):—*Diarthrodactylæ*, *homœophyllæ*, *macro-dactylæ*, *flabellatæ*, *gymnocarpæ*.

Tirupane, 9th Nov. 1895, no. 23.

In the absence of fruit I have been unable to label this, but think that it

cannot well belong to any of the foregoing species. It is an extremely slender graceful plant with lax whorls (attaining a diameter of 4 cm.) and long internodes. The branchlets are usually 3, occasionally 4, times furcate, the rays gradually diminishing in length, the primary about half that of the entire branchlet. The dactyls are about 25μ in diameter, the ultimate cell being long, slender, and acute. There are a few young antheridia on the specimen, the only one Mr. Blow was able to find.

CHARA CORALLINA, Willd. in Mém. Acad. Roy. Sc. Berl. 1803 (1805) p. 89.

Jungle-pool, near Kandy, 5th Nov. 1895, no. 25; shallow tank, Tangalla, 8th Jan. 1898, no. 40. Two sterile plants collected at Tirupane, 7th & 9th Nov. 1895, nos. 26 & 27, apparently also belong to this species.

The plant from Kandy has on the older parts well-developed fruits, the oospores measuring about 825μ long, 550μ thick (excl. ridges); on the younger branches small antheridia. The plant from Tangalla has well-developed antheridia (diameter c. 500μ) but no matured oospores.

C. corallina was previously collected in Ceylon by Trimen.

C. FLACCIDA, Braun in Hooker's Journ. Bot. i. (1849) p. 296.

At sea-level near Panadura, 16th Nov. 1895, no. 28 (no ripe fruit); shallow tank, Tangalla, 8th Jan. 1898, no. 41; paddy-field, near Dikwella, 9th Jan. 1898, two forms, nos. 42 & 43.

There is often considerable difference in the length of the stipulodes, even on the same plant. In one of the forms from Dikwella (no. 43) they are all extremely short and the spine-cells are minute, in these respects agreeing with *C. psilopitys*, Braun. The branchlets are usually short with only 3-4 segments, the oospores are short and broad and of a very dark brown, in marked contrast to the golden-brown of those of the Tangalla plant, which is typical of *C. flaccida*.

C. HYDROPITYS, Reichenb. in Mössler's Handb. ed. 3 (1834) p. 1670; Braun in Hooker's Journ. Bot. i. (1849) p. 296.

Near Dikwella, 9th Jan. 1898, no. 44.

A small-fruited form, the oospores being hardly 300μ long.

This species was apparently first collected in Ceylon by Wichura in 1862, see Braun & Nordst. 'Fragmente,' p. 135.

C. ZEYLANICA, Willd. in Mém. Acad. Roy. Sc. Berl. 1803 (1805) p. 86.

Negumbo, at sea-level, 13th Nov. 1895 (sterile), no. 29; shallow tank, Tangalla, 8th Jan. 1898, no. 45; Dikwella, 9th Jan. 1898, nos. 46 & 47; Amblangoda, 12th Jan. 1898, no. 48.

In some of the Dikwella specimens, fruits are produced at the lowest branchlet-nodes, in others and in those from Tangalla and Amblangoda the



M. Groves del.
P. Highley lith.

C. Hodges & Son imp.

NITELLA LEPTODACTYLA sp. nov.

lowest node is sterile. This character used in the key to Braun and Nordstedt's 'Fragmente' to divide the numerous varieties of this species into two primary sections does not appear to be an entirely satisfactory one. The coronula varies from nearly straight in the Dikwella plant to broadly spreading in that from Tangalla. The oospore of the Dikwella plant is about 600μ long, that of the Tangalla and Amblangoda plants as much as 725μ . The anterior bract-cells exceed the fruit, being in some cases nearly double the length. The spine-cells are short (longest in the Tangalla plant) and on some stems scarcely visible.

This species was first discovered in Ceylon by Lebeck in 1798. It was collected by Trimen in 1881 in Colombo Lake and at Belligam on the south coast.

EXPLANATION OF PLATE 6.

Nitella leptodactyla, J. Groves.

Fig. 1. Plant, natural size.

2. Base of whorl, showing one complete branchlet; $\times 6$.

3. Ultimate furcation of branchlets showing dactyls and young gametangia; $\times 20$.

4. } Apices of dactyls; $\times 70$.

5. }
6. Oogonium; $\times 70$.

7. Apex of oogonium with coronula: $\times 110$.

8. Oospore; $\times 70$.

(The magnifications are only approximate.)

The Pollination of the British Primulas.

By MILLER CHRISTY, F.L.S.

[Read 1st December, 1921*.]

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I.—Introductory Remarks.

FORTY years or so ago, one often heard or read papers dealing with some special point in connection with the pollination (then called "fertilization") of flowers by insects. At that time, the whole subject was practically new, having recently been brought to the front as a result of the superb experimental and observational work of Darwin. Since then, the chief problems involved have been solved, largely through the labours of our past-President, Sir John Lubbock (afterwards Lord Avebury), Alfred W. Bennett, John Scott, the Rev. George Henslow, I. H. Burkill, and others in this country, but mainly through the work of German observers, two of whom have published almost-encyclopædic works on the subject. Yet there is still much to be learned in detail as to the means by which the flowers of certain plants secure pollination.

Of few plants, if of any, is this more true than it is of the British members of the genus *Primula*. Indeed, the precise means by which the flowers of these plants (especially the Primrose) secure adequate pollination has long been, and still remains, a complete mystery, though there has been much discussion, and close attention has been given to it by many observers, including Darwin †, T. R. Archer Briggs ‡, Hermann Müller §, myself ||,

* Revised slightly May 1922.

† Journ. Linn. Soc., Bot. x. (1869), pp. 437-454, and 'Different Forms of Flowers on Plants of the same Species,' pp. 22, 36, &c. (1877).

‡ Journ. of Bot. (Seemann's), viii. (1870), pp. 190-191; Trans. Plymouth Instit. iv. (1872), pp. 180-190; and 'Flora of Plymouth,' p. 279 (1880).

§ 'Die Befruchtung der Blumen durch Insekten,' pp. 346-347 (Leipzig, 1873), and 'The Fertilization of Flowers,' transl. and ed. by Prof. D'Arcy W. Thompson, pp. 383-386 (Lond., 1883).

|| See *post.*, p. 107 n.

Prof. Rugero Cobelli *, John French †, Alexander H. Gibson ‡, G. F. Scott-Elliott §, I. H. Burkill ||, Dr. Paul Knuth ¶, Rev. E. Bell **, Prof. F. E. Weiss ††, Prof. G. S. Boulger †‡, Miss Mary L. Armitt §§, the Rev. E. T. Daubeny |||, E. G. Highfield ¶¶, and A. A. Dallman ***. One of these devoted most of a large part of a fair-sized volume to a discussion of the problem, but without, I think, contributing anything material to its solution; nor does the latest contribution to the subject (that of Mr. Dallman), though painstaking, carry it much further, so far as I can see.

That so much observation and discussion should have produced so little result is not altogether surprising; for the problem presents (as will be found) certain unusual complications. There are some plants whose flowers exhibit a highly complicated floral mechanism (the Orchids, for example); yet the manner of their pollination is fairly obvious. On the other hand, the dimorphic heterostyled flowers of the *Primulas* exhibit a floral mechanism which, though highly ingenious, is comparatively simple †††; yet (as has been stated) the precise manner of their pollination has defied investigation and remains to this day unexplained. It may be doubted, indeed, if there is any problem of the kind more puzzling than that which has been called "the Mystery of the Primrose."

Three species of the genus *Primula* are immensely abundant in Britain, though one of them is so in one district only. All three species are also very common and very widely distributed on the Continent. They are:—

* Verhändl. der K. K. zool.-bot. Gesellsch. in Wien, xlii. (1893), pp. 73-78.

† Essex Naturalist, v. (1891), pp. 120-124.

‡ Trans. Bot. Soc. of Edinb. xix. (1893), p. 156.

§ Flora of Dumfriesshire, p. 114 (1896).

|| Journ. of Bot. xxxv. (1897), p. 186.

¶ Handb. der Blütenbiologie, ii. (1899), pp. 308-319 (Leipzig, 3 vols., 1898-1905), and Handb. of Flower Pollination, transl. by Prof. J. R. Ainsworth Davis, iii. pp. 64-75 (Oxford, 3 vols., 1906-09).

** 'The Primrose and Darwinism,' by a Field Naturalist [i.e., E. B.], (Lond., 1902).

†† New Phytologist, ii. (1903), pp. 99-105; iii. (1904), pp. 168-171; and Nature Notes, xv. (1904), pp. 103-106.

†‡ Nature Notes, xv. (1904), pp. 84-86.

§§ New Phytologist, iii. (1904), p. 170.

||| Nature Notes, xvi. (1905), pp. 116 & 136-137.

¶¶ Knowledge, xxxix. (1916) pp. 113-117.

*** Journ. of Botany, lix. (1921), pp. 316-322 & 337-345.

††† It was, however, Darwin's opinion that *tri*-morphic heterostyled flowers, such as those of *Lythrum Salicaria*, present "a more extraordinary and complicated arrangement of the reproductive system than can be found in any other organic beings". (see his Introd. Note to Müller's 'Fertilization of Flowers,' p. ix).

- (1) The Primrose (*P. vulgaris* Hudson, vel *acaulis* Linn.),
- (2) The Cowslip (*P. veris* Linn., vel *officinalis* Jacquin),
- (3) The True Oxlip (*P. elatior* Jacquin)*.

On the distribution, distinctive features, and other peculiarities of these three species, as observable in Britain, I have already published two lengthy papers †.

The question as to how the pollination of our Primulas is effected was first raised by Darwin. Between 1862 and 1868, he read before the Linnean Society five papers ‡, in which he pointed out clearly and conclusively the significance of heterostylism, especially as exemplified in the Primulas §. Later, these papers, collected and revised, appeared in the form of a work dealing comprehensively with the whole subject, as then known ||. In the course of his investigations, Darwin naturally made observations to ascertain what insects effect the pollination of the Primrose and the Cowslip ¶; and the results of these observations require notice at the outset.

Of the Primrose, he wrote, in 1869 **, that it "is never visited (and I speak after many years' observation) by the larger humble bees, and only rarely by smaller kinds: hence its fertilization depends almost exclusively on moths"—a statement the first portion of which is certainly incorrect, 'as Darwin himself afterwards came to see. Much nearer the truth, though still somewhat short of it, is his final statement ††—

It is surprising how rarely insects can be seen during the day visiting the flowers, but I have occasionally observed small kinds of bees at work. I suppose, therefore, that they are commonly fertilised by nocturnal Lepidoptera.

* As all three are very well known by their vulgar names, I use these in speaking of them hereafter. There are also two other British species of the genus—*P. farinosa* Linn. and *P. scotica* Hooker; but of these, though they are covered by my title, I have nothing to say. Nor have I anything to say of the various hybrids into which all three species enter, each with both the others: namely *P. vulgaris* × *veris* (the "Common Oxlip"), *P. vulgaris* × *elatior*, and *P. elatior* × *veris*.

† (1) Trans. Essex Field Club, iii. (1884), pp. 148-211, and (2) Journ. Linn. Soc., Bot. xxxiii. (1897), pp. 172-201.

‡ All afterwards published in its Journal (Bot.), vols. vi., vii., and x.

§ "Heterostylism" is the term he used, and it is preferable to, because more definite than, "heteromorphism," a term suggested by Asa Gray and used by Lubbock and some later writers.

|| 'The Different Forms of Flowers on Plants of the same Species' (London, 8°, 1877).

¶ Darwin records no similar observations on the Oxlip, a plant he probably never saw growing wild.

** See Journ. Linn. Soc., Bot. x. (1869), p. 438.

†† 'Forms of Flowers,' p. 36 (1877).

Of the Cowslip, Darwin wrote in 1862* :—

What insects habitually visit Cowslips, as is absolutely necessary for their regular fertility, I do not know. I have often watched them, but perhaps not long enough; and only four times I have seen humble-bees visiting them. One of these bees was gathering pollen from short-styled flowers alone; another had bitten holes through the corolla; and neither of these would have been effective in the act of fertilization. Two others were sucking long-styled plants.

Here, again, we find Darwin's earliest statement incomplete and valueless. Later, he extended and amended it several times †. His final statement ‡ is to the effect that—

The flowers of the cowslip and of the other species of the genus secrete plenty of nectar; and I have often seen humble-bees, especially *B. hortorum* and *muscorum*, sucking the former in a proper manner, though they sometimes bite holes through the corolla. No doubt moths likewise visit the flowers, as one of my sons caught *Cucullia verbasci* in the act §.

These observations of Darwin's were (for him) remarkably incomplete; for, as a fact, insects visit the flowers of our *Primulas* much more frequently than he realized.

In a problem of such complexity, there is, I submit, no more hopeful means of reaching a solution than that of summarizing and reviewing in detail all the evidence available, in the hope that one may thereby guide some other observer into the right track; and this, precisely, is my present aim.

II.—*Observations on Insect Visitors.*

In three Tables which follow (each relating to a particular one of the three species of *Primula* concerned), I set forth in detail the results of my own personal observations, extending over rather more than forty years, on the different species of insects accustomed to visit each species. After each Table, I add, in brief, the observations of similar kind which have been recorded by others.

Comment on all these various observations appears in Section VI.

* Journ. Linn. Soc., Bot. viii. (1862), p. 85.

† See, for instance, *idem*, x. (1869), p. 438.

‡ 'Forms of Flowers,' p. 22 (1877).

§ This is a common British moth, flying at dusk during April and May, when the Cowslip is in flower (see *post.*, p. 116).

TABLE I.—THE PRIMROSE (*P. vulgaris*).

No. of Obsvn.	Date.	Locality and Insect Visitors observed.
	1882.	
1	Mar. 8.	Garden, Chignal St. James, Essex.—A Hive Bee (<i>Apis mellifica</i> L.), after rejecting the flowers of a red Primrose, visited 14 ordinary Primroses (some of them twice) on four plants growing close together, but seemed to find a difficulty in reaching the nectar and rejected some flowers altogether.
2.	Mar. 15.	Westley Wood, Saffron Walden, Essex.—A small dark Bee (<i>Anthophora acervorum</i> L.) visited rapidly 4 or 5 flowers, growing near together, and seemed to gather nectar from each.
3.	Apr. 7.	Lawn Wood, Langley, Essex.—Saw two Humble Bees (? sp.) rise from flowers, as I approached them, having apparently visited the flowers.
	1883.	
4.	Apr. 5.	Westley Wood, Saffron Walden.—About noon, on a fine hot day, I saw a Sulphur Butterfly (<i>Gonepteryx rhamni</i> L.) visit five flowers on as many plants, also a Small White Butterfly (<i>Pieris rapæ</i> L.) visit one flower and then fly away, also a medium-sized Humble Bee (<i>Bombus</i> sp.) visit two flowers on one plant, 1 on another plant, hover over others, and then visit several more, finally flying right away. (There were no flowers, other than Primroses, in bloom in the wood at the time.)
5.	Apr. 9.	Westley Wood (as above).—Saw two Humble Bees of the same species (both of which I caught) visit many flowers.
6.	May 1.	Hyde Wood, Little Yeldham, Essex.—About noon, on a hot day, in a sheltered cut-down part of the wood, I saw a Bee (<i>Anthophora acervorum</i> L. ♂) visit many flowers of the hybrid <i>P. vulgaris</i> × <i>elatior</i> ; also another, of same species, but more inconstant, visit in succession 16 Primroses, 5 Violets, 1 Primrose, 4 Violets, 9 Primroses, and 1 Violet—36 flowers altogether; also a large, black, orange-banded Humble Bee (<i>Bombus</i> sp.) visit several Primroses and afterwards various flowers of <i>Scilla nutans</i> , <i>Viola</i> , and <i>Ranunculus Ficaria</i> ; also another (<i>Bombus</i> ? sp.) visit 18 flowers of Primrose and <i>P. vulgaris</i> × <i>elatior</i> , but reject 2 Oxlips (<i>P. elatior</i>) on one plant; also various other Bees (? <i>A. acervorum</i>) visit many Primroses; also several Bee-flies (<i>Bombylius</i> sp.) visit various Primroses.
	1884.	
7.	Mar. 16.	Roadside bank, Doddington, Essex.—Saw a Sulphur Butterfly (<i>Gonepteryx rhamni</i> L.) visit one Primrose.
8.	Apr. 3.	Wood, Laindon, Essex.—Saw several Bees (? <i>A. acervorum</i> L. and another species) and many Bee-flies (<i>Bombylius</i> sp.) busy visiting Primroses, which were very abundant.
	1906.	
9.	Apr. 13.	Garden, Chignal St. James, Essex.—Saw a small blackish Bee (? <i>Anthophora acervorum</i> L.) visit 6 or 8 Primroses in quick succession, when I disturbed him by trying to catch him.
	1907.	
10.	Mar. 31.	Bushy Wood, Broomfield, Essex.—During the afternoon of a hot bright day, in a sheltered out-down portion of the wood, where there were practically no other flowers out, I watched many Humble Bees, of at least three species, also (I believe) a few Hive Bees, and many Bee-flies (<i>Bombylius</i> sp.); all very busy visiting Primroses with remarkable constancy—due, no doubt, to the absence of other flowers. I saw a Humble Bee (? <i>B. hortorum</i>) visit 68 Primroses in rapid succession; also another (? same species) 131 Primroses similarly. (These two Bees, when visiting many flowers on the same plant, crawled actively from one flower to another, and occasionally pulled open a partly-expanded flower.) I saw also four smaller blackish Bees, one of which visited 18 Primroses; another (? the same individual) 8 Primroses, another

No. of Obsvn.	Date.	Locality and Insect Visitors observed.
	1907 cont.:—	62 Primroses; and another 90 Primroses—all with absolute constancy. Two other, medium-sized, brownish Bees visited, respectively, 27 and 22 Primroses—both with absolute constancy. Many of the foregoing Bees hovered over, but rejected, many Primroses (? long-styled); while, on the other hand, on several occasions, I saw a Bee visit a second time a flower it had recently visited.
11.	Apr. 13.	<i>Wood, Roxwell, Essex.</i> —Between 4 and 5 p.m., in a cut-down portion, I watched a fair number of Bees, of two species, visit a fair number of Primroses. Five individuals of one species, small, blackish, and very active in movement (? <i>Anthophora acervorum</i> L.), visited, respectively (1) 20 Primroses and then two Cowslips (these growing close together), (2) 9 Primroses (after which a similar Bee arrived and the two flew off together), (3) 102 Primroses in quick succession, (4) (? the same individual) 67 Primroses, also in quick succession (after which, she alighted on a stump to re-arrange her load of pollen, subsequently flying away), and (5) 47 Primroses. Three individuals of the other species, larger and striped (<i>Bombus</i> sp.), visited, respectively, (1) 2 Primroses, (2) 18 Primroses, on several different plants, and (3) 8 Primroses.
12.	Apr. 18.	<i>Same wood as No. 11.</i> —A fine day, but a cold N.E. wind blowing. Extremely few Bees visiting the same Primroses, which, though still in flower in vast numbers, have passed their best.
13.	Apr. 19.	<i>Broom Wood, Chignal, Essex.</i> —I caught two large Humble Bees (<i>Bombus pratorum</i> and <i>B. terrestris</i>) visiting Primroses.
14.	Apr. 19.	<i>Same wood as Nos. 11 and 12.</i> —At midday, with a cool wind blowing, I saw a few Bees (<i>Anthophora acervorum</i> and <i>Bombus</i> sp.) and one or two Bee-flies (<i>Bombylius</i> sp.) visiting the same Primroses, now still further past their best.
15.	Apr. 26.	<i>Same wood as Nos. 11, 12, and 14.</i> —Saw several middle-sized Bees (? <i>Anthophora acervorum</i>) and one of a smaller species (<i>Andrena gwynana</i>) visiting the same Primroses (now almost over) with constancy.
16.	1915. May 2.	<i>Broom Wood, Chignal, Essex.</i> —Captured one <i>Bombus agrorum</i> ♀ visiting Primroses.
17.	1916. Apr. 9.	<i>Broom Wood, Chignal.</i> —During the morning, in an open ride, I watched a shabby (evidently hibernated) Peacock Butterfly (<i>Vanessa io</i> L.), which visited, within a few minutes, 20 or more Primroses (several of them more than once), on five or six different plants, quite obviously sucking nectar from most of them.
18.	Apr. 23.	<i>Same wood.</i> —Twice, during the day, in a sheltered hollow in which grew a great many Primroses, I saw a Peacock (<i>Vanessa io</i> L.)—perhaps the same individual—visit 5 or 6 Primroses in quick succession.
19.	1917. May 7.	<i>Same wood.</i> —The Primroses are now at their best (a month later than usual), but I have not yet been able to detect one single insect of any kind visiting them, though I have watched—this being due, doubtless, to the extremely-cold unpleasant weather which prevailed during the preceding weeks.
20.	1918. Mar. 4.	<i>Same wood.</i> —A fine, still, warm day. Saw a Peacock (<i>Vanessa io</i> L.) visit 1 Primrose. Later, saw another visit 7 Primroses in fairly-quick succession.
21.	Apr. 22.	<i>Same wood.</i> —In a sheltered glade, watched a Sulphur (<i>Gonepteryx rhamni</i> L.) visit 9 Primroses in fairly-quick succession. An hour later, in an adjacent glade, watched another (or, perhaps, the same) visit 7 Primroses on adjacent plants and depart after searching very obviously, but without success, for more.
22.	1922. May 6.	<i>Meadow, Pleshey, Essex.</i> —Watched a large Humble Bee (<i>Bombus lapidarius</i>) busy visiting Primrose flowers.

Observations by others on the various insects which visit the PRIMROSE have been recorded in considerable numbers. It is, therefore, surprising that Müller should have said not a single word on the insect visitors to this species*.

Knuth's observations, made near Kiel, were, however, fairly ample, and he gives † the following list of insects :—

HYMENOPTERA.

Bombus hortorum L., ♀ working busily and effectively.

Anthophora acervorum (L.) (= *A. pilipes* F.), ♀, ditto, but less often.

Apis mellifica L.; one "visited several flowers in succession," and apparently obtained some nectar.

LEPIDOPTERA.

Gonepteryx rhamni (L.), fairly frequent.

Vanessa urticae (L.), "flying persistently from flower to flower, 21.iv.'96, sucking very vigorously"; "evidently succeeded in getting a part of the nectar."

Mr. T. R. Archer Briggs made observations in the neighbourhood of Plymouth, and the following list is compiled from his record ‡ :—

HYMENOPTERA.

Anthophora acervorum (L.) (= *A. pilipes* F.), "often."

Andrena gwynana Kir., gathering pollen abundantly.

Bombus ? sp.

DIPTERA.

Bombylius medius (L.), § "often."

LEPIDOPTERA.

Gonepteryx rhamni (L.), "occasionally."

Prof. Giovanni has observed || that, in Italy, the flowers are visited by *Gonepteryx rhamni* (L.).

Prof. Bernardino Halbherr has observed || that, in Italy, the following beetles are found in the flowers :—

<i>Anthobium robustum</i> H.	} All, no doubt, eating the pollen.
<i>Brachypterus gravidus</i> Ill.	
<i>Meligethes umbrosus</i> St.	
<i>Meligethes erythropus</i> Gyll.	

Signor Mario Bezzi records || that, near Milan, the flowers are frequented by *Bombylius medius* (L.).

* In his 'Fertilization of Flowers' (1883). Possibly the plant does not grow in the neighbourhood of Lippstadt, where he lived.

† 'Flower Pollination,' iii. (1909), p. 69.

‡ See *ante*, p. 105.

§ The species observed was probably *B. discolor*, not *B. medius*.

|| *Fide* Cobelli (see *ante*, p. 106 n.).

Mr. I. H. Burkill, speaking of the Yorkshire coast, says * that the nectar of the Primrose "is beyond the reach of all bees which are on the wing at its flowering season, except *Bombus hortorum*."

Mr. G. F. Scott Elliot states † that, in Dumfriesshire, the visits of *Bombus hortorum* to the Primrose are "regular and sufficient" to pollinate its flowers.

Mr. Hugh Richardson, of Newcastle, informs me that, early in May 1881, he saw a humble-bee visit four flowers on three different plants growing near together; also that he has seen a bee visit the "Hybrid Oxlip," *P. vulgaris* × *veris* ‡.

The Rev. E. Bell writes §:—

In all our experience, we have never seen a humble-bee, either of the larger or of the smaller kinds, visiting the flowers. . . . Four insects, and four insects only, with a long proboscis, and each on a *single occasion only*, have we seen visiting the Primrose and probing for honey. . . . This was our experience after seeing and examining thousands and thousands, we might say millions, of the flowers.

Such a meagre result suggests that the observer's eyesight was defective. The four species he saw were—

HYMENOPTERA.

Anthophora acervorum (= *pilipes*), seen on 27 April, visiting inconstantly both Primrose and *Viola canina*.

DIPTERA.

Bombylus discolor.

LEPIDOPTERA.

Gonepteryx rhamni, seen on 19 April.

Pieris brassicæ, ditto.

The evidence of the Rev. E. T. Daubeny is wholly negative. He says ||:—
During the last two springs, I have kept this flower under special observation at all sorts of odd times, including evening and early night. No bees or flies with long proboscis have been seen by me visiting it by day, and no Noctuæ or thick-bodied moths by night. This is corroborated by two members of my family who have assisted in the matter.

More complete and systematic than most of the foregoing were the observations of Prof. Weiss ¶, made specially (as he says) to remove the "considerable amount of uncertainty [which] exists as to the manner in which the pollination of the Primrose is effected":—

* Journ. of Botany, xxxv. (1897), p. 186.

† 'Flora of Dumfriesshire,' p. 114 (1896).

‡ See Trans. Essex Field Club, iii. (1884), p. 195.

§ 'Primrose and Darwinism,' pp. 30-31 (1902).

|| Nature Notes, xvi. (1905), p. 136; see also p. 116.

¶ New Phytol. ii. (1903), pp. 99-105, and iii. (1904), pp. 168-170.

About 15 April 1903, near Church Stretton, in Shropshire, he watched two large patches of Primroses, growing in a fairly-sheltered position, on the sides of a narrow lane, staying for from half-an-hour to an hour, between 11 A.M. and 1 P.M., on eight successive days. Further, on two of these days, he made observations at two other stations also. The weather was unfavourable throughout, being windy and cold; and he remarks on the extent to which the number of insects upon the wing on any particular day depended on the temperature. The combined result of all his observations was as follows:—

HYMENOPTERA.

Bombus terrestris, 7 individuals seen *; very inconstant, visiting other flowers (*Leontodon*, *Salix*, *Viola*, and *Potentilla Frugariastrum*) more often than Primrose.

Anthophora acervorum (L.) (= *pilipes* F.) †, ♀ and ♂, 12 individuals seen; more constant to the Primrose.

Apis mellifica L., 3 individuals seen; appeared on warm days only and was unable, apparently, to reach the nectar.

Andrena gwynana K., numerous individuals seen; gathered pollen greedily from short-styled flowers.

DIPTERA.

Bombylius major (L.), 20 individuals seen; the most active visitor, especially on warm days.

At the beginning of April 1904, the Professor continued his observations at another locality in North Staffordshire; but, though he watched on three mornings, he saw no insects at work, except *Bombylius*—doubtless because the weather was again cold.

Miss Mary Armitt, on 19 April 1904, “a thoroughly summer-like day,” watched Primroses ‡ near the foot of Nab Scar, Westmorland, and saw *Bombylius major* busy among them. One visited 2 short-styled flowers on one plant, then 2 long-styled flowers on another plant. Another visited flowers on a short-styled plant, then others on a long-styled plant. On a later day, another visited 10 flowers—1 on one plant, 4 on a second, 3 on a third, and 2 on the fourth.

Between 1911 and 1919, Mr. A. A. Dallman made a number of very careful observations, many of them *by night*, at several places in North Wales, and he received help from Miss E. Bray, of Hailsham, in East Sussex, who made other observations, all of them by day, in her district. Between them, they observed and record § a considerable number of insect and other visitors to the Primrose, and these were all identified carefully by competent authorities.

* The number of *visits* paid by each of the various insects is not recorded.

† Recorded originally, in error, as *A. furcata*.

‡ See New Phytologist, iii. (1904), p. 170.

§ Journ. of Botany, lix. (1921), pp. 316-322 & 337-345.

The most striking feature of Mr. Dallman's observations in North Wales seems to be the extreme fewness of the bees and other flying insects he saw visiting the Primrose there, as compared with the number one sees visiting them elsewhere. For instance, he saw no single Hive Bee visit any Primrose flower (not even when flowers grew within a few yards of some hives), though many individuals were busy visiting other species of flower. In Sussex, however, Miss Bray seems to have seen bees at work in about the numbers usual elsewhere. Among the few day-flying insects seen by these two observers, but not noted by earlier observers, are:—

DIPTERA.

Hyetodesia lucorum Flin.

Lucilia cæsar (L.).

HYMENOPTERA.

Halictus leucopus Kirby, ♀.

Mr. Dallman's extensive *nocturnal* observations, made with the aid of an electric flash-lamp, revealed no single species of flying insect as visiting the flowers, but showed that they are visited (or, rather, *frequented*) during the night by a remarkable number of creatures belonging to several different Orders, as follows:—

ARACHNIDA.

Trombidium? sp.

Meta segmentina Clk.

COLEOPTERA.

Adrastus limbatus Fabr.

Barynotus obscurus Fabr.

Epurea longula Er.

Meligethes difficilis Sturm.

M. erythropus Gyll.

M. exilis Sturm.

M. flavipes Sturm.

M. maurus Sturm.

M. picipes Sturm.

M. viridescens Fabr.

Otiorhynchus ligneus Oliv.

O. picipes Fabr.

Rhagonycha fuscicornis Oliv.; common; feeding on pollen.

Sciaphilus muricatus Fabr.

Tachyporus chrysomelinus (L.).

T. hypnorum (L.).

T. solutus Er.

GASTROPODA.

Helix hispida L.; feeding on the corolla.

Helix? sp.; ditto ditto.

Limax agrestis L.

Limax? several sp. } abundant; eating the stigma, pollen, and corolla.

HEMIPTERA.

Drymus brunneus Sahlb.

ISOPODA.

Oniscus asellus L.

Porcellio scaber Latr.

ORTHOPTERA.

Forficula auricularia N.; common; feeding on pollen.

THYSANOPTERA.

Tæniothrips ? sp.*

Without doubt, many other nocturnal "visitors" of this kind might be observed. I have myself frequently seen signs that slugs or snails had eaten both anthers and petals, as shown by their slime left on the latter and the mutilation they had effected †. Occasionally, too, I have found a small grub in the corolla-tube, apparently about to pupate therein. But, of these and of other similar accidental visitors, I have taken no account ‡.

TABLE II.—COWSLIP (*P. veris*).

No. of Obsvn.	Date.	Locality and Insect Visitors observed.
	1882.	
1.	April 19.	Railway bank, Newport, Essex.—A reddish Humble Bee (<i>Bombus</i> sp.) visited several flowers.
2.	May 5.	Meadow, Roxwell, Essex.—Watched a considerable time, surrounded by a large number of flowers, without seeing a single Bee visit them, though the day was warm and Bees were busy visiting other flowers around.
3.	May 6.	Meadows, Roxwell, Essex.—Watched similarly, among many flowers, in several places, but saw only one single large striped Humble Bee (<i>Bombus</i> ? sp.), which visited a number of flowers on a cluster beside a ditch, but left when I tried to capture it.
	1883.	
4.	May 1.	Roadside hedge, Tilbury-by-Clare, Essex.—A Sulphur Butterfly (<i>Gonepteryx rhamni</i>), searching diligently for flowers of any kind, visited one Cowslip flower, took a long flight, returned, visited 10 more Cowslip flowers, but left when I tried to capture it.

* Mr. Dallman regards all the foregoing as "visitors" to the Primrose. To me, it seems that one might as well include the wandering cow which casually gobbles up half a plant and, in so doing, by shaking the flowers (as a passing rabbit might also do), may accidentally pollinate some of them to some slight extent.

† See Trans. Essex Field Club, iii. (1884), p. 194.

‡ Prof. Weiss has expressed his belief (see *New Phytol.* ii. p. 104) that the Primrose may be pollinated to a certain extent by the agency of the wind. The Rev. E. Bell has expressed ('*Primrose and Darwinism*,' pp. 90 & 186) a somewhat similar view. I believe, however, that, in the case of all the three *Primulas* in question, the amount of pollination (if any) effected by the agency of the wind is so small as to be wholly negligible.

No. of Obsvn.	Date.	Locality and Insect Visitors observed.
	1914.	
5.	April 26.	Meadows, Roxwell, Essex.—On a warm sunny morning, after watching from 10.30 till 12.15, among many Cowslips in full flower, I saw only six Bees (3 <i>Bombus hortorum</i> L., ♂, and 3 <i>Anthophoru acervorum</i> L.) at work on them
6.	May 3.	Meadow, Roxwell, Essex.—Watched for over an hour among many Cowslips (still out fully, but rather past their best) without seeing a single Bee visit any of them, probably because a cold wind was blowing.
7.	May 10.	Hedge bank, Writtle, Essex.—A large Humble Bee (? <i>Bombus lapidarius</i> L., ♀) visited several flowers in a sheltered spot.

Records of observations on insect visitors to the COWSLIP are few. The most complete are those of Knuth *, made near Kiel, but his list is a little more than an amplification of that of Müller †, made in Thuringia. Knuth enumerates :—

HYMENOPTERA.

Bombus hortorum F.

Bombus agrorum F., ♀, sucking.

Anthophora acervorum (L.), ♂ and ♀, frequent, sucking.

Andrena gwynana K., ♀, in large numbers, collecting pollen from short-styled flowers, but soon leaving long-styled flowers.

Halictus albipes F., ♀, as *A. gwynana*.

Halictus cylindricus F., ♀, ditto.

DIPTERA.

Bombylius discolor Mg., sucking.

LEPIDOPTERA.

Gonepteryx rhamni (L.).

COLEOPTERA.

Meligethes ? sp., eating pollen.

Darwin has recorded ‡ the capture of a Mullein Moth, *Cucullia verbasci*, in the act of visiting a Cowslip flower.

Prof. Weiss, early in April 1904, in North Staffordshire, watched Cowslips § in two meadows in which they were abundant. In one, which was very exposed, he saw no insects at work ; but, in the other, which was sheltered by a copse, he saw five Humble Bees (some *Bombus muscorum* F., others *B. terrestris* L.), "each of which visited quite a large number of flowers."

* 'Flower Pollination,' iii. (1909), pp. 67 & 69.

† Nature, 10 Dec., 1874, p. 111 n. In his earlier 'Fertilization of Flowers,' p. 385, he had mentioned "humble-bees and *Anthophora pilipes*" only.

‡ See ante, p. 108, and post., p. 135.

§ New Phytologist, iii. (1904), p. 170.

TABLE III.—OXLIP (*P. elation*).

No. of Obsvn.	Date.	Locality and Insect Visitors observed.
	1881.	
1.	April 21.	<i>Pounce Hall Wood, near Saffron Walden.</i> —Watched a large Humble Bee (? <i>Bombus hortorum</i>) working very systematically, for a considerable time, among countless flowers, in a sheltered spot. He first visited every flower on one umbel; then every flower on every umbel on the same plant; then flew to the next nearest plant, which he treated in the same way; and so on till I lost sight of him.
	1882.	
2.	March 29.	<i>Pounce Hall Wood.</i> —Watched a similar Humble Bee (? <i>B. hortorum</i>) at work on the flowers very diligently and systematically, though it was late in the evening and raining slightly.
3.	March 30.	<i>Pounce Hall Wood.</i> —Watched a good many Bees at work busily on the flowers, though it was late in the evening. There were three species at least—a few of the large Humble Bee (? <i>B. hortorum</i>), a good number of a smaller species (? <i>Andrena gwynana</i>), and a single one of a still smaller Bee (? <i>Apis mellifica</i>).
4.	April 10.	<i>Dow Wood, Lindsell, Essex.</i> —Watched one or two blackish Bees (? <i>Anthophora acervorum</i>) at work on the flowers.
5.	April 10.	<i>Meadows beside river at Gt. Bardfield, Essex.</i> —Watched a blackish Humble Bee (? <i>Anthophora acervorum</i>) at work very busily and systematically. I saw him visit 108 flowers consecutively, rejecting many, but without even hesitating at the flowers of any other species, though various other early spring flowers were out in some abundance close at hand.
6.	April 11.	<i>Woods near Thaxted, Essex.</i> —On a hot bright morning, I watched three species of Bee and one of <i>Bombylus</i> busily at work on the flowers in a sheltered glade in Avesey Wood. Of the Bees, the Honey Bee (<i>Apis mellifica</i>) seemed the most numerous. Some were visiting Oxlips and others Violets (there being no other flowers out adjacent); but, in either case, individuals seemed to be quite constant, either to one species or the other. The other two species were Humble Bees (? <i>B. hortorum</i> and <i>Anthophora acervorum</i>), and seemed to be present in about equal numbers. I watched two of these Bees (one of each species) which seemed to be visiting, quite indifferently, both Oxlips and Violets, both of which were out abundantly, but practically no other flowers. In two other adjacent woods, I watched the same species all busily at work, in a similar way. One Honey Bee visited 23 Oxlip flowers consecutively, when I caught him. In one of these woods, I saw also a Sulphur Butterfly (<i>Gonepteryx rhamni</i>) visit three flowers consecutively and then fly around them for some time.
7.	April 16.	<i>Peverell's Wood, Wimbish, Essex.</i> —Watched several large Humble Bees belonging to two species (? <i>B. hortorum</i> and <i>B. muscorum</i>) at work, both in cut-down and thinly grown-up portions of the wood.
	1883.	
8.	April 7.	<i>Peverell's Wood.</i> —A fine bright day. Many Bees, of five or six sorts, busy visiting the Oxlips.
9.	April 8.	<i>Great Hales Wood, Ashdon, Essex.</i> —A similar day. Humble and other Bees, of similar sorts, busy visiting Oxlips.
10.	April 30.	<i>Wood, Wethersfield, Essex.</i> —A bright hot day. Watched a number of Bees and Bee-flies at work quite busily on a great profusion of flowers in a sheltered recently-cut portion. There were several species of Humble Bee, one Hive Bee, and some <i>Bombylus</i> (? <i>B. discolor</i>).

No. of Obsvn.	Date.	Locality and Insect Visitors observed.
11.	1883. May 1.	Wood at Yeldham, Essex.—Another bright hot day. About noon, watched many large Bees at work on flowers. One (? <i>Anthophora acervorum</i>) visited many flowers of <i>P. elatior</i> × <i>vulgaris</i> quite constantly. Another (? <i>Bombus hortorum</i>) was far less constant, visiting (apparently quite indifferently) 18 flowers of <i>P. elatior</i> and <i>P. elatior</i> × <i>vulgaris</i> , but rejecting two flowers of pure <i>P. elatior</i> on one plant.
12 & 13.	1910. April 8–12.	Woods (two) at Falden and Sosoye, Belgium.—Watched, in company with Messrs. G. A. and E. Boulenger, a number of Bees (including <i>Anthophora acervorum</i> , <i>Bombus lapidarius</i> , and <i>B. terrestris</i> var. <i>lucorum</i>) busily at work on the Oxlips, which were abundant and in full flower in cut-down portions.
14.	1914. April 18.	Wood, Chignal St. James, Essex.—Watched a remarkably-inconstant large Humble Bee (<i>Bombus</i> sp.) visit 6 flowers of <i>Narcissus</i> and 2 of <i>P. elatior</i> (planted there by myself), all growing close together; after which he flew right away.
15.	1915. April 14.	Small wood, Saling, Essex.—Watched, in company with Mr. C. E. Salmon, various Hive Bees (<i>Apis mellifica</i>) busily visiting Oxlips growing in a boggy portion. One visited 16 flowers quite constantly before we lost sight of him.

As to the OXLIP: no one, except myself (so far as I know), has observed its insect visitors in this country*; but the observations of both Müller† and Knuth‡, made in Germany, are very full. Their lists are practically identical:—

HYMENOPTERA.

Bombus hortorum L., ♂ ♀, abundant, sucking normally and collecting pollen.

Bombus sylvarum L., ♀, sucking normally.

Bombus lapidarius L., ♀, ditto.

Bombus confusus L., ♀, ditto.

Bombus terrestris L., ♀, ditto.

Anthophora acervorum (L.), ♂ ♀, abundant, sucking and collecting pollen.

Osmia rufa (L.)

Apis mellifica L. } Both attempting to suck, but soon ceasing to do so.

Andrena gwynana K., ♀, abundant, collecting pollen from short-styled flowers (only).

DIPTERA.

Bombylius discolor Mg., abundant, sucking.

Bombylius major (L.), much less frequent; probably unable, in most cases, to reach the nectar.

* Mr. C. Nicholson informs me that in Peverell's Wood, Essex, in April 1914, he saw *Bombus ruderatus* Fabr. visiting it.

† 'Fertilization of Flowers,' pp. 384–385 (1888).

‡ 'Flower Pollination,' iii. p. 66 (1909).

LEPIDOPTERA.

Gonepteryx rhamni (L.), fairly often.

COLEOPTERA.

Homalium florale Payk., abundant, creeping about the flowers.

In regard to the Bee-flies, belonging to the genus *Bombylius*, already mentioned several times : at least three species (two British and one Continental) visit all three species of *Primula* so freely that they deserve special notice here.

These insects, though very bee-like in general appearance, belong to the Diptera*. They are adapted—in the main, at all events—for sucking nectar. This they do by means of a long thick proboscis, which is carried permanently stretched out straight in front of the insect, even during flight, and is never coiled, as in the case of bees†. This proboscis is quite long enough to reach the nectar of (and, therefore, to pollinate effectively) at least the smaller flowers of all our *Primulas*; and there can be no doubt that (as Prof. Weiss has remarked) this insect is “an active agent in the pollination of the Primrose”‡.

The *Bombylii* come abroad in April and May, when both the Primrose and the Oxlip are in bloom. To the former, at any rate, they are remarkably constant, seldom visiting any other flower, as Prof. Weiss has remarked§. I have very often watched the insect at work. In Devonshire, Archer Briggs says that one species “often” visits the Primrose, from which it “seems to obtain a great deal of its food.” Knuth|| says that all the three species visit the flowers, “but only those with a particularly-long proboscis are able to get at the nectar.” Very much to the point are the remarks of Prof. Weiss, who says, as a result of his observations already described¶, that *Bombylius major*—

was the most regular of all the visitors [the others being four species of Bee], having been observed on seven days out of the eight; and, on the occasion when he was not observed, I think this was due to my visit being earlier than usual (*i.e.*, before 11 A.M.), [when] a fresh wind from the north-west was blowing.

The *Bombylii* show amazing activity, even for insects, their movements being rapid in the extreme. An individual, when visiting *Primula* flowers, does so after the graceful manner of the humming-bird hawk-moth, hovering for a time, almost motionless, just above the flower, its thick straight proboscis fully extended, and its wings vibrating so rapidly as to be almost invisible.

* I have elsewhere spoken of them, in error, as Hover-flies (*Syrphidæ*).

† Müller says (*Fertil. of Flowers*, p. 43) that their probosces are fitted “for boring into succulent tissues” and that they “restrict themselves to the juices of flowers;” but Major E. E. Austen, of the British Museum (who has kindly assisted me with information), doubts whether they are capable of being used for any such purpose.

‡ *New Phytol.* ii. p. 101.

§ *Op. et loc. cit.*

|| ‘*Flower Pollination*,’ iii. pp. 66-71.

¶ *New Phytol.* ii. (1903), pp. 100, 101.

Generally, though not always, the insect inserts its proboscis into the opening of the corolla-tube and remains, as though sucking nectar, for a brief period; after which it dashes away so suddenly and swiftly that the eye often fails to tell which way it went, and one has to look again at the flower to make sure that it has really gone. Often the creature appears to dash off in this lightning-like manner even before it has inserted its proboscis. It is not surprising that an insect distinguished by such a remarkable habit should have gained for itself, as it has in Pembrokeshire, the name of "Primrose Sprite"*. Further, so motionless can it hover that, even when it has inserted its proboscis into the corolla-tube, one often remains in doubt whether it has actually alighted on the flower or is still hovering. My own observations lead me to believe that sometimes it *does not alight at all* when so engaged. Archer Briggs asserts † that an individual he watched visiting Primroses "rested its fore feet on the corolla, but kept the wings vibrating." The precise observations of Prof. Weiss are conclusive that sometimes, at any rate, it does actually alight on the flower.

In almost every instance [he says‡] when it visited the primrose, I saw this graceful insect ultimately settle on the flower, and, after its wings had come to rest, push its head as far as possible down the corolla-tube, and remain in that position for some time. . . . After visiting a few primroses (three or four) on the earlier colder days, and as many as eighteen or twenty in warmer weather, *Bombylius* rested on a dead leaf, well protected by its colouring, and cleaned off the pollen-grains that were adhering to its head and proboscis.

Other small creatures which also visit (or perhaps one should say frequent) the flowers of all our *Primulas* (as noticed above) may also, for convenience, be treated together here. They comprise several minute beetles and a Thrips. These are all robbers of either pollen or nectar, or of both, or else suckers of the sap of the plant; and all of them seem to *inhabit* the flowers, rather than to visit them merely.

Of these small creatures, by far the most frequent is a very small beetle, *Meligethes picipes* Sturm, which regularly frequents the flowers of all three species, but especially those of the Primrose, sheltering in the tubes of their corollas§. It is a smooth, shiny, black, thick-set insect, 1½–2 mm. long, 1 mm. broad, and about the same height. In Essex, I have met with it abundantly (indeed, practically always) whenever I have had occasion to

* See Major R. O. Latham, in *Nature*, 5 May, 1921, p. 301.

† Trans. Plymouth Inst. iv. (1872), p. 189.

‡ New Phytol. ii. (1903), p. 101.

§ This beetle was identified for me, many years ago, by the late Mr. T. R. Billups (see Trans. Essex Field Club, iii. (1884), p. 196 n.) and his identification has been confirmed recently by the kindness of Mr. K. G. Blair, of the British Museum. The genus *Meligethes* contains many closely-allied species, nearly all pollen-eaters. They frequent chiefly the flowers of the Compositæ, especially those of *Hieracium* and *Taraxacum*; but, in spring, they are to be found in the flowers of many widely-differing plants.

examine flowers of either the Primrose or the Oxlip (but especially the former), provided the weather has been warm and sunny, and the state of development of the flowers such that the anthers of many plants were dehiscing actively. On such occasions, one can count (in the case of the Primrose, at any rate) on finding at least one beetle in nearly every tube, several in many tubes, and six or seven in some; while, on one occasion, I saw *at least ten* in a single tube*. Yet on cold wet days, or very early or very late in the flowering-season, before the anthers have begun to dehisce or after they have finished, one sees very few of these beetles†. In the flowers of the Cowslip (which, unlike the two other species, grows largely in the open), the beetle is met with much less commonly—perhaps because, at the time the Cowslip flowers, there are also in flower many other species of plant on whose pollen and nectar the beetle may feed.

How regular and widespread is this beetle's habit of frequenting the flowers of *Primula* may be gathered from the fact that, apart from my own observations on it in Essex, the Rev. M. C. H. Bird‡ and the Rev. E. T. Daubenys§ have both found it abundantly in Primroses in Norfolk|| and Burkill in Yorkshire¶; whilst Mr. Dallman has found it and other members of the genus in Primroses in North Wales**. On the Continent, I have seen it (or some very similar species) in Oxlips in Belgium; Müller has seen it (or some other member of the genus) in Cowslips in Thuringia††; Knuth mentions it as occurring in the Primrose in Schleswig-Holstein‡‡; and Cobelli has recorded the occurrence of two other members of the genus (*M. umbrosus* and *M. erythropus*) in Primroses in Italy§§.

Yet some observers have failed to detect the presence of this beetle in the flowers—possibly because either it does not occur in their districts or the weather was unfavourable at the time of their observations. Thus, Darwin does not mention having seen it, though he mentions having seen Thrips, which are much smaller creatures. The Rev. E. Bell also failed to observe

* In a wood near Saffron Walden, on 5 April, 1883.

† For instance, on 15 April, 1905, the Rev. E. T. Daubenys found them in 40 per cent. of a number of Primrose flowers he examined; but, on 8 May following, in the same flowers, he could find none (see Nature Notes, xvi. p. 116).

‡ Nature Notes, xv. (1904), p. 96.

§ *Op. cit.*, xvi. (1905), p. 116.

|| Both record the species as *Eusphalerum primulae*, an identification which is probably erroneous, though this species does frequent Primroses and other flowers in spring and early summer. It is a small, rather elongated, black and brown beetle, 2–3 mm. long, and it is common locally, but I am not familiar with it as a frequenter of Primroses in Essex, though Burkill noted it in Yorkshire.

¶ Journ. of Botany, xxxv. p. 179.

** Journ. of Botany, lix. (1921), p. 320 *et seq.*

†† Nature, 10 Dec., 1875, p. 111 n.

‡‡ 'Flower Pollination,' iii. p. 549.

§§ Verhandl. zool.-bot. Gesellsch. Wien, xlii. (1893), p. 78.

it, in spite of his very extensive examination of Primrose flowers*, in which he found innumerable Thrips. More extraordinary still, Prof. Weiss failed to find any beetles in the Primroses he watched in Shropshire, though he looked for them†. Their absence was due, probably (as he himself suggests), to the cold weather.

In addition to eating pollen, *Meligethes picipes* also consumes nectar. Possibly, indeed, its main object in visiting *Primula* flowers is to steal their nectar‡. On many occasions, I have seen single individuals (and often several together) right down at the bottom of the corolla-tube, busily gathering nectar from the nectaries. To reach these, the beetles have, of course, to traverse, in either form, the entire length of the corolla-tube; and this they are able to accomplish. Yet they do not accomplish it without a certain amount of difficulty; for there is not sufficient space between the stigma and the side of the corolla-tube in the short-styled flowers or between the style and the anthers in the long-styled flowers to allow a beetle to squeeze through without some struggling and, consequently, some stretching of the corolla-tube or some pressing together of the anthers, or both of these. It will be understood readily that, as a result of all this struggling to squeeze past or between the anthers, the beetles become thickly dusted with pollen all over, in spite of their smooth glossy surface. Under the microscope, it may be seen adhering abundantly to their antennæ, head, thorax, body, and legs. They are often, indeed, so profusely covered with it as to appear yellow, rather than black. They seem to regard the anthers as their natural habitat; for, on several occasions, when I have torn open the corolla-tube of a long-styled flower, I have seen the pollen-covered beetles inhabiting it run to the anthers and try to hide beneath them—conscious, no doubt, that, owing to protective colour-resemblance, they could hide safely among them.

Another point in connection with these small beetles is the fact that they fly well and readily take flight, especially when disturbed. I have seen them take flight from my hand and also actually from the limb of the corolla. They are thus able to pass with ease from plant to plant. Again, if turned on their backs, they open their wings and elytra to right themselves, which they achieve with ease.

In addition to *Meligethes picipes*, certain other minute beetles have been observed in Primrose flowers. Thus, in Italy, four species (including two other species of *Meligethes*) have been seen in them§; in Germany, Müller

* See 'Primrose and Darwinism' (1902).

† New Phytologist, ii. (1903), p. 104.

‡ At all events, the late Mr. Edward Rosling, F.R.M.S., who kindly examined microscopically for me the contents of the stomachs of several individuals, could find therein no trace of pollen.

§ See *ante*, p. 111.

has observed *Homalium florale**; and in North Wales, Mr. Dallman has found over a dozen other species in the flowers at night †.

Further, Mr. Dallman has shown ‡ that, at night, Primroses are visited by various spiders, earwigs, slugs, snails, and wood-lice.

Yet other, and still more minute, creatures which frequent the flowers of both Primrose and Oxlip are Thrips—very small, slender, elongated, blackish, partially-winged insects, scarcely one millimetre in length, belonging to the genus *Teniothrips* of the order *Thysanoptera*. These are often found in abundance on the leaves and petals of plants, especially roses, carnations, and chrysanthemums. They are probably all sap-suckers, and often do much injury to the plants on which they live. To some extent, perhaps, they also consume pollen. In *Primula* flowers, I have seen them often, but always in very small numbers—generally a single one or a pair. Darwin ‡, the Rev. E. Bell §, and Mr. Dallman † all speak, however, of having seen Thrips abundant in Primroses. The latter says they appear “to occur wherever the Primrose is met with.” Possibly Thrips enter the flowers largely for shelter, though one species (*T. primulae*) seems to be associated sufficiently closely with the genus *Primula* to have been named after it.

III.—*The Depths of the Corolla-tubes of the Flowers.*

Before considering what bearing the foregoing observations have upon the problem in hand, it is necessary to ascertain the average depths of the deep and narrow corolla-tubes of the flowers of *Primula*. This matter has a very intimate bearing on the problem; for upon the depths of the corolla-tubes naturally depends the ability or inability of visiting insects to reach the nectar and to pollinate the flowers.

In all the three species, the depth of the corolla-tube differs in the two forms of flower; for the tubes of short-styled flowers are slightly deeper than those of long-styled flowers. This fact has been overlooked entirely by British botanists, even by Darwin; but several Continental botanists have recorded their observations on the point. I summarize their results separately for each species:—

Primrose.—The most satisfactory measurements are those of Cobelli, made in the Tyrol ||, which show that the average depth of ten short-styled flowers was 19.1 mm.: that of ten long-styled flowers, 17.7 mm.—a difference of 1.6 mm.

My own measurements have been made in Essex. In April 1916, I found that six short-styled and six long-styled flowers each averaged 16.1 mm.; but the number

* See *ante*, p. 119.

† Journ. of Botany, lix. (1921) pp. 320–322.

‡ ‘Forms of Flowers,’ pp. 23, 37, 49, &c.

§ ‘Primrose and Darwinism,’ pp. 33–36, &c.

|| Verhandl. zool.-bot. Gesellsch. Wien, xlii. (1892), p. 74.

of flowers measured was too few to yield reliable results. In May 1922, I found that, of 25 short-styled flowers gathered in a wood, two measured 15 mm., three 17, five 18, three 19, ten 20, and two 22—an average of 18·9 mm.; while, of 25 long-styled flowers, one measured 14 mm., one 15, one 16, ten 17, five 18, five 19, and two 20—an average of 17·6 mm. and a difference of 1·3 mm.

Burkill's measurements, made near Scarborough*, showed that the depth was 15–20 mm.; but he did not discriminate between the two forms.

Knuth's measurements, made in Schleswig-Holstein†, gave an average of about 20 mm. in both forms; for he also did not discriminate.

Cowslip.—The only measurements I know of are my own, made in Essex. In April 1916, I found that the average depth of ten short-styled flowers was 15·1 mm.; that of twelve long-styled flowers, 15 mm.—a very small difference. In May 1922, I found that, of five short-styled flowers of the larger form which grows on hedge-banks, one measured 15 mm., one 16, two 17, and one 18—an average of 16·6 mm.; while, of nine long-styled flowers belonging to the same form, two measured 14 mm., three 15, one 16, two 17, and one 18—an average of 15·7 mm. and a difference of 0·9 mm. On the same date, of 24 short-styled flowers belonging to the slightly smaller form which grows in meadows, ten measured 15 mm., one 16, ten 17, one 18, and two 19—an average of 16·3 mm.; while, of 25 long-styled flowers of the same form, one measured 14 mm., thirteen 15, seven 16, two 17, and two 18—an average of 15·6 mm. and a difference of 0·7 mm.

Oxlip.—As to the flowers of this plant, there are on record measurements by three trustworthy Continental observers.

Errera's measurements, made near Brussels in 1878‡, are the earliest and most reliable, being the result of the measurement of a very large number of flowers. They show that the average depth in short-styled flowers was 15·2 mm.; in long-styled flowers, 13·6 mm.—a difference of 1·6 mm.

Müller's measurements, made in Germany§, show that the depth of short-styled flowers was 15–17 mm.: that of long-styled flowers, 12–14 mm.—a difference of 3 mm.

Knuth's measurements, made in Schleswig-Holstein||, are identical with Müller's.

My own measurements, made in Essex, show that the average depth of seven short-styled flowers was 16·3 mm.: that of five long-styled flowers decidedly less, but the exact figure was unreliably recorded.

While these results differ considerably among themselves, they suffice, nevertheless, to show clearly that the corolla-tubes of short-styled flowers are really, on an average, considerably (usually 1–3 mm.) deeper than those of long-styled flowers.

* Journ. of Botany, xxxv. (1897), p. 186.

† 'Flower Pollination,' iii. (1909), p. 68.

‡ Rec. de l'Inst. Bot. vi. (1905), p. 229; and 'Œuvres Bot.' i. (1908), p. 242.

§ 'Fertilization of Flowers,' p. 384 (1883).

|| 'Flower Pollination,' iii. (1909), p. 65.

¶ Possibly, indeed, he is merely quoting Müller's figures.

It should be remembered, however, that the size of a flower and the depth of its corolla-tube vary greatly in both forms, according to the vigour of the plant bearing it, which depends mainly on the favourable or unfavourable nature of the situation in which the plant happens to grow*.

IV.—*The Tongue-lengths of the Insects known to visit the Flowers.*

The average tongue-lengths of known insect visitors will be found appended (so far as I have been able to ascertain them) to the name of each insect mentioned in the lists given in the following Section†.

It will be recognized that, as in the case of the depths of corolla-tubes, the lengths of the tongues of visiting insects varies considerably in different individuals—at least 2–4 mm. in the case of the larger species of *Bombus*. There is, therefore, no fixed and absolute rule enabling one to say that any particular species of insect is or is not capable of reaching the nectar of (and, therefore, of pollinating) any particular species of *Primula*.

Nevertheless, one is able to say this with practical certainty in the case of certain species of insects which have been seen to visit the flowers—namely, most of the larger humble-bees (some eight or ten species belonging to the genera *Bombus* and *Anthophora*), four species of butterfly, and one species of moth; for all these have tongues ranging from 10 mm. to 21 mm. in length, and are thus able to reach the nectar of most of the flowers of all the three species. There are also a few smaller bees (some four or five in number, belonging to the genera *Bombus* and *Apis*), as well as at least two species of bee-fly (*Bombylius*), which have tongues ranging from 7 mm. to 12 mm. in length; and these are able to reach the nectar of some of the smaller flowers of probably all the three species.

Further, one must bear in mind that, for a bee to reach the nectar of any *Primula* flower, it is not necessary for it to possess a tongue of the full length of the corolla-tube of that flower; for the heads of some bees are elongated and tapering, and thus may be inserted into the mouth of the corolla-tube

* Thus, it would certainly be found that, in the Oxlip, the average size of both forms of flower on the Alps (where the plant grows in the open) is less than in flowers in this country (where the plant usually grows in woods and is more luxuriant on that account).

† For these, I have been obliged to rely almost wholly on the measurements given by Müller and Knuth; for British writers have strangely avoided this subject. Thus, Saunders, who published an elaborate paper on the tongues of British bees (*Journ. Linn. Soc., Zool.* xxiii. pp. 410–432), does not give one single measurement. The matter, though important from the present point of view, is of little value to the systematist; for, owing to the great variation in the sizes of individuals in many species of bees, both ♀ and ♂ (this depending on the available food-supply), tongue-lengths also vary much, and are, consequently, of little value as specific characters. For advice on this point, I am indebted to the kindness of Dr. R. C. L. Perkins, F.R.S., Dr. James Waterston, F.E.S., and Mr. W. H. Tams, F.E.S.

to a distance (in some species) of as much as 3 or 4 mm. This is especially the case with flowers of the short-styled form, the "throat" (or entrance to the corolla-tube) of which is expanded to a depth of from 3-4 mm. This (being about equal to the difference in depth between the tubes of the two forms) places the two forms very much on an equality so far as the visits of bees are concerned.

V.—*Summary of Observations on Insect Visitors.*

The observations, by myself and others, set forth in Section II, prove beyond dispute that all our three species of *Primula* are visited not uncommonly, during the day, by a fair number of different species of insects, some of which are sufficiently long-tongued to be capable of pollinating their flowers effectively.

At first sight, it might seem that this fact alone, once definitely established, ought to suffice to solve the whole problem. Unfortunately, it will be found that this is, for several reasons, very far from being the case. One must, therefore, consider in detail how the foregoing observations bear upon the problem. For this purpose, it is necessary to summarise them; and this is attempted in the following paragraphs.

The observations in question show that about fifty-five species of insect and other small creatures have been recorded as visiting or frequenting the flowers of our three species of *Primula*, namely:—

Arachnida	2 species.
Coleoptera	20 species (about).
Diptera	5 species (about).
Hymenoptera	16 species (about).
Hemiptera	1 species.
Lepidoptera	6 species.
Orthoptera	1 species.
Thysanoptera	1 species.
Isopoda	2 species.
Gastropoda	3 species (about).
<hr/>	
Total	57 species (about).

Of these species, however, at least one-third may be disregarded, inasmuch as they are not "visitors" in the true sense, but robbers, which frequent the flowers, mainly at night, with the object of feeding on either nectar, or pollen, or the actual substance of the corolla. These may be disregarded for present purposes; for, if they effect pollination at all, it is by chance merely and certainly to a negligible extent only. No one can regard them as having been intended by nature (so to speak) to effect regularly and normally the pollination of the flowers.

Examining the observations in detail, it will be found that all visiting insects worth considering in this connection (about thirty) may be arranged roughly in four groups, as follows :—

Group 1.—Those insects, all very active and fairly large, which have tongues sufficiently long (not less than, say, 10 mm. in length) to enable them to reach the nectar and, therefore, to pollinate the flowers effectively and in the regular manner. They, in number about fifteen, form one-third of all the insects known to visit the flowers. They comprise six or eight of the larger bees, three bee-flies, five large butterflies (which emerge from hybernation in the earliest days of spring), and one moth.

The bees are—

- Bombus hortorum* (tongue 18–21 mm.), a frequent visitor to all three species ;
- Bombus agrorum* (tongue 10–15 mm.), recorded as visiting Cowslips ;
- Bombus muscorum* (tongue 10–14 mm.), ditto ;
- Bombus sylvarum* (tongue 12–14 mm.), recorded as visiting Oxlips ;
- Bombus lapidarius* (tongue 12–14 mm.), ditto ;
- Bombus confusus* (tongue 12–14 mm.), ditto ;
- Bombus* (probably several other species) ;
- Anthophora acervorum* (tongue 19–21 mm.), a very frequent visitor to all three species.

The three bee-flies are—

- Bombylius major* (tongue 10 mm.) ; *Bombylius discolor* (tongue 11–12 mm.) ;
- Bombylius medius* (tongue —? mm.).

All very frequent visitors, those with the longer tongues being certainly able to reach the nectar*.

The five butterflies are—

Gonepteryx rhamni (tongue 18 mm.), a regular visitor, though in small numbers, to all three species, but especially to the Primrose. I have seen it visit all three, and Knuth saw it do so on one single day (26 April, 1896) in Germany. It has been seen visiting the Primrose in Devonshire and in Italy. As a visitor to the Primrose, it is, of necessity, fairly constant ; for, when that plant is in flower, there are few others out for it to visit.

Vanessa io (tongue 15–16 mm.). I have seen this as an occasional and very constant visitor to Primroses growing in sheltered woodland rides in Essex, but to neither of our two other Primulas ; not recorded, I believe, by any other observer.

Vanessa urticae (tongue 14–15 mm.), seen by Knuth visiting Primroses (“flying persistently from flower to flower”) on one occasion (21 April, 1896) in Schleswig-Holstein.

- *Pieris brassicae* (tongue 15 mm.), one seen by Rev. E. Bell to visit Primrose ; not otherwise recorded.

Pieris rapae (tongue 13–18 mm.), seen once by myself on 4 April 1883, visiting Primrose ; not otherwise recorded.

* See *ante*, p. 119.

The moth is—

Cucullia verbasci (tongue about 20 mm.), one caught visiting a Cowslip flower; not otherwise recorded.

Group 2.—Those insects (limited to three or four medium-sized bees) which have tongues too short (that is, less than 10 mm. in length) to permit of their reaching the nectar of any flower of ordinary size, though long enough to permit of their reaching it in the case of small ill-developed flowers (which, therefore, they may pollinate). Such are—

Bombus terrestris (tongue 7–9 mm.), a frequent visitor.

Apis mellifica (tongue 6–7 mm.), a not uncommon visitor to the flowers of both Primrose and Oxlip, but not (so far as I have seen) to those of the Cowslip. I have watched individuals visiting, with fair constancy, many flowers of both species, though other individuals were less constant, interposing visits to *Viola* and other flowers. Most appeared to be sucking normally and successfully, though some may have been gathering pollen only. Both Müller and Knuth state that they have seen it visit the Oxlip, but that it soon abandons the attempt to suck.

Osmia rufa (tongue 7–8 mm.), recorded by Müller and Knuth as attempting to suck, but soon abandoning the attempt.

Group 3.—Those medium-sized, very active, pollen-gathering bees (limited to three or four species) which have tongues far too short to enable them to reach the nectar, but gather large quantities of pollen from flowers of the short-styled form (only). Such are—

Halictus albipes (tongue — mm.);

Halictus cylindricus (tongue 3–4 mm.);

Andrena gwynana (tongue $2\frac{1}{2}$ mm.), probably the most frequent of all bee visitors to all three species, from which it gathers pollen greedily. As Archer Briggs has remarked*, it may often “be seen on these flowers with its posterior tibia loaded with golden masses.” Müller says†:—“It holds the anthers in the mouth of the flower with its fore feet, bites the pollen loose with its mandibles, and sweeps it with the tarsal brushes of the mid legs into the collecting-hairs of the hind legs.”

Group 4.—Those insects (limited to certain species of very small beetles and one species of Thrips) which, lacking tongues of any kind, obviously can never effect pollination in the regular and orthodox manner, but apparently do so in an irregular and unorthodox manner. Such are—

Meligethes picipes extremely abundant in the corolla-tubes of the flowers, which they seem to *inhabit*, rather than visit merely‡;

* Trans. Plymouth Inst. iv. (1872), p. 189. † ‘Fertilization of Flowers,’ p. 385.

‡ See *ante*, p. 120.

Eusphalerum primulae, abundant, but less frequently and more locally ;
 Various other minute beetles ;
Tentothrips primulae, frequent in the corolla-tubes*.

VI.—Critical Remarks on the Observations.

In view of the foregoing, the casual critic may well ask :—Are not the visits of all these numerous insects amply sufficient to ensure the adequate pollination of the flowers of all our three *Primulas*? At first sight, one would certainly conclude that they are ; but, the more one looks into the matter, the more one comes to see that they are not.

In examining in detail the evidence in support of this statement, it will be found convenient to work backwards, considering in the reverse order the four groups of insect visitors already described.

Of the small insects included in *Group 4*, by far the most important is the minute beetle, *Meligethes picipes*, which is quite obviously incapable of pollinating the flowers of either form in the regular and orthodox manner. Yet there seems every probability that it is quite capable of pollinating (in fact, actually *does* pollinate, though irregularly) the flowers of all our three *Primulas* to a considerable extent, not only illegitimately, but also even legitimately—as effectively, in fact, as this could be done by any long-tongued insect inserting its proboscis and sucking the nectar in the regular and orthodox manner †.

Take the case of one of these beetles alighting upon (say) a long-styled flower. At once it enters the corolla-tube, squeezing past the stigma, upon which it leaves inevitably some of the pollen with which it is dusted (some of which will have come, almost certainly, from some short-styled flower previously visited) ; then, descending the tube to the nectaries, it squeezes past the anthers, dusting itself with more long-styled pollen ; next, returning upwards, it again squeezes past the anthers, dusting itself with more long-styled pollen ; finally, it flies away to another plant, which we may assume to be short-styled (for it is as likely to be that as not). Entering the corolla-tube, the beetle squeezes between the anthers, dusting itself freely with short-styled pollen ; descends the tube, squeezing past the stigma, on which it will inevitably leave some of the pollen brought from the long-styled flower previously visited ; next it reaches the nectaries ; returning, after feeding, it again squeezes past the stigma, on which it leaves more pollen ; finally, after squeezing again between the anthers, it again flies away to

* See *ante*, p. 123.

† That the beetle is capable of doing this has been held by others, including Prof. F. E. Weiss (see *Nature Notes*, xv. p. 106) and E. T. Daubeney (see *Nature Notes*, xvi. p. 110).

another plant (which, as likely as not, will be long-styled), to repeat the cycle all over again.

Yet, surely, it is quite impossible to accept seriously the view that the flowers of any species of *Primula* can be *intended* to be pollinated, in an irregular, casual, and even accidental manner, by a small beetle or any similar insect. If such were the case, it would be hard to explain how the remarkable phenomenon of heterostylism could ever have originated, what necessity there can ever have been for it, and what use it can be now; for, in that case, all its highly-specialized arrangements for ensuring cross- (as against self-) pollination would be no more than a highly ingenious and most interesting, but entirely useless, complication. Nature does not lay herself out, however, to produce useless curiosities of the kind or to play mere aimless pranks. All she does, she does with some definite object. Therefore, as heterostylism exists (and I see no reason whatever to regard it as a survival merely), it must serve some useful purpose; and that purpose can only be (so far as anyone has yet been able to show) the one so clearly pointed out by Darwin.

Nevertheless, it seems certain (as stated above) that the flowers of all our three *Primulas* are, in fact, pollinated freely—almost, it seems, as a matter of course—by these minute beetles, in a manner in which the highly-ingenuous contrivances pertaining to heterostylism obviously play little or no part. How, then, are we to explain this perplexing fact?

To me, it seems that the only conclusion one can come to is that the irregular pollination effected by the beetles is superfluous and accidental (probably, even, injurious, in view of the large amount of pollen and nectar stolen by them in the course of their operations), and that it is merely supplementary to (though possibly greater in volume than) the pollination effected by large long-tongued insects, in the manner obviously intended*.

In regard to Thrips†: it seems probable that they also, like *Meligethes*, may be capable of effecting pollination, both legitimately and illegitimately, but, of course, in an irregular manner. Darwin concluded that these insects might effect the *self*-pollination of both forms of flower to a small extent‡. The Rev. E. Bell even regarded Thrips as the insect which normally pollinates the Primrose§; which seems to me inconceivable. But, even

* The whole case of this irregular pollination of *Primula* flowers by *Meligethes* seems more or less on a par with that of a gang of burglars who, while breaking into one's house, stealing one's silver, and drinking one's whisky, nevertheless render one (quite unintentionally and unknown to themselves) a definite service of some value, though a service one did not desire—would, in fact, rather have been without—because one possessed previously a means of securing the performance of that service in a more effectual manner and through a more regular and acceptable medium.

† See *ante*, p. 123.

‡ 'Forms of Flower,' pp. 23, 37, 49, &c.

§ 'Primrose and Darwinism,' pp. 34–36, &c.

admitting that Thrips are capable of effecting pollination, the amount of such pollination must be exceedingly small, owing to their minute size and the fact that they are not known to be capable of a flight of sufficient length to enable them to pass from plant to plant*.

As to the few small pollen-eating bees forming *Group 3*: they are all quite incapable of effecting the pollination of the flowers in the regular and orthodox manner. They are all robbers merely, and their frequent visits to the flowers are made solely for the purpose of stealing pollen. Their visits are, therefore, prejudicial, rather than beneficial, to the plant.

Nevertheless, it seems certain that these bees do pollinate the flowers effectually, to a certain extent, but *those of the long-styled form only*, and even those only in an irregular and unorthodox manner. Thus, the pollen they gather must come entirely from flowers of the short-styled form (in which the anthers are exposed at the mouth of the corolla-tube); for, in flowers of the long-styled form, the anthers are placed too far down the tube to be accessible to them. If, however, one of these bees, having visited a short-styled flower and become dusted with its pollen, happens to visit, even momentarily, a long-styled flower (in which the stigma is exposed in the mouth of the corolla-tube), there is a probability that it may leave some pollen upon (and thus effectually pollinate it); but this cannot take place in the case of short-styled flowers (in which the stigma is situated far down the tube and is quite inaccessible to the bee).

Of the last-named of these bees, *Andrena gwynana*, Müller, after stating that it gathers pollen from short-styled flowers only, adds† that—

It visits the long-styled form also, but flies away immediately—not, however, without performing cross-fertilization in the momentary visit. I have never seen a pollen-collecting humble-bee alight on a long-styled flower. It seems to recognize them at a distance and to avoid them‡.

Prof. Weiss, in the course of his observations in Shropshire§, noticed that, from short-styled flowers, this bee gathered the pollen greedily and, in getting at it, poked its head deep into the mouth of the corolla. It naturally [he adds] stayed longer in the short-styled flowers, but its movements in the long-styled forms [?flowers] were sufficient to pollinate the protruding stigma.

From this, he concludes that these bees are “very active agents of cross-pollination of the Primrose”—a conclusion I am quite unable to accept.

* See Bell, ‘Primrose and Darwinism,’ pp. 35, 36.

† ‘Fertilization of Flowers,’ p. 385 (see *ante*, p. 118).

‡ If this is really so, these bees, in their visits to the flowers of *Primula*, are “constant,” to a certain extent, to one *form*, just as most insects, when visiting other flowers, are constant, more or less, to one *species*.

§ New Phytol. ii. p. 103 (see *ante*, p. 112).

As to the small bees forming *Group 2*: there can be no doubt that they can, and actually do, pollinate some of the flowers. Nevertheless, it is certain that the number of occasions on which they do this are few—so few that one cannot possibly suppose they can pollinate adequately the flowers of any of our *Primulas*.

Further, certain of these short-tongued bees (being unable to reach the nectar in the ordinary manner, by way of the entrance to the corolla-tube), have been observed to bite a hole in the side of the tube, just above the level of the top of the calyx—a proceeding which enables them to steal the nectar, but without effecting pollination, unless, possibly, of the short-styled flowers. Darwin observed this, many years since, in the case of the Cowslip *. Knuth says † that, in Germany, the flowers of this species are “fairly often perforated by humble-bees.” Müller says ‡ of *Bombus terrestris* (tongue 7–9 mm.) that it

makes a hole in the corolla-tube [of the Oxlip], a little above the calyx, sometimes biting it with its mandibles, sometimes piercing it with its maxillæ, and so reaching the honey with its tongue. I have sometimes seen this bee, before boring the flower, make several attempts to reach the honey in the legitimate way.

Jules Macleod, in 1880, watched this operation being performed on Oxlips by two species of *Bombus* (one not named: the other given as *B. muscorum*, but more likely *B. terrestris*), in the woods near Ghent, in Belgium. In some woods, he says §, it was hard to find a flower the tube of which had not been perforated: in other woods quite near, scarcely a flower had been pierced—the difference depending, he says, on the abundance or scarcity of the bee he identifies as *B. muscorum*. He adds that, by listening, it was not difficult to hear the noise made by the bee whilst tearing the hole in the corolla-tube.

Prof. Weiss, on two occasions in the spring of 1903, observed humble-bees, “not sucking at the flower [of Primrose], but moving all over the corolla, both at the front and at the back of the flower, apparently endeavouring to obtain the honey by illegitimate means.” ||.

It is only when we come to consider the large long-tongued humble-bees and butterflies forming *Group 1* that we find ourselves dealing at last with a fair number of insects (about fifteen species), all of which are known to visit the flowers in fair numbers and are fully capable of pollinating them effectively. That they actually do the latter to an appreciable extent can not be doubted.

* See *ante*, p. 108.

† ‘Flower Pollination,’ iii, p. 66.

‡ ‘Fertilization of Flowers,’ p. 384.

§ Bull. Acad. Roy. Belge, n. s., l. (1880), p. 30.

|| See New Phytologist, ii. (1903), p. 102.

Yet these long-tongued insects visit the flowers so comparatively seldom that it is difficult to believe that even they can pollinate *adequately* any of the three species.

To obtain confirmation of this view, one has only to take one's stand, on some day in early spring, in some cut-down wood, with Primroses or (in a certain district) Oxlips in flower all around one in such countless thousands that they make the ground appear covered with a vast carpet of pale yellow *, and then to watch. If the day be cold, wet, or windy (as are most days in early spring), one may wait for half-an-hour or longer without seeing even one single insect visiting the flowers. If, however, the day happens to be warm and bright, one may count on seeing quite a number of bees of several species, a good many bee-flies, and an occasional butterfly, all at work on the flowers. Yet, even so, one will observe almost invariably that the bees are engaged much more busily in visiting the few other flowers (*Salix*, *Viola*, *Ranunculus Ficaria*, *Nepeta Glechoma*, &c.) which are in flower at this early period, and that the crowd of bees buzzing round these forms a striking contrast to the few visiting the vastly-more-numerous *Primula* flowers.

Or take the case of the Cowslip :—One may take one's stand in a meadow, early in May, at the height of the plant's flowering season, with hundreds of its blossoms in sight around ; yet, even on a fairly warm and sunny day, one may watch for, perhaps, ten or fifteen minutes before seeing even a single bee visiting a flower ; and, on a cold windy day, one is likely to see none at all. This species is visited by insects less often, I think, than either of the other two—perhaps because, when it flowers (which it does rather later than they), there are many other flowers of many species in bloom.

It is clear, therefore, that the long-tongued insects belonging to *Group 1*, though they can (and, in fact, do) pollinate the flowers in the regular and orthodox manner, nevertheless visit them (as stated already) in small numbers and comparatively seldom—so seldom, in fact, that one is driven to the conclusion that such sparse visitation cannot possibly suffice to effect, regularly and adequately, the pollination of any plants so immensely abundant and so extremely free-flowering as are all the three *Primulas*.

I myself reached this conclusion many years since, and it has been reached independently by others who have studied the subject †. Thus, Mr. I. H. Burkill, after watching Primroses for many hours on the Yorkshire coast,

* I have given elsewhere (see *Trans. Essex Field Club*, iii. p. 181 n.) figures which seem fully to support an estimate that, in favourable circumstances, a cut-down wood may produce at least about 70,000 plants of *P. elatior*, bearing at least about 210,000 umbels, to an acre. In the case of *P. vulgaris*, the number of plants and of flowers would probably be even larger.

† An exception to this view is that of Mr. Scott Elliot, who says (see *ante*, p. 112) that, in Dumfriesshire, the visits of *Bombus hortorum* are "regular and sufficient" to pollinate the flowers—a conclusion which may be doubted in the absence of fuller details.

concluded * that "None of the insects seen on it . . . [was] sufficient for its fertilization." Mr. John French, a good field observer, has remarked on the apparent "absence of fertilizing agents." † The somewhat-imperfect observations of the Rev. E. Bell and the more complete ones of Prof. Weiss, point strongly in the same direction. Still more to the point are the remarks of the Rev. E. T. Daubeny, who says ‡, after carefully watching Primroses during two springs :—"I am . . . impressed with the way ordinary insect visitors of our spring flowers neglect the Primrose. . . . If its fertilization depended upon them, the primrose would soon cease to exist."

The position now reached seems to be this :—On the one hand, the long-tongued insects which are obviously capable of pollinating effectively the flowers of our Primulas, and seem clearly intended to do so, visit the flowers, to all appearances, too seldom to effect their pollination adequately. On the other hand, the flowers are frequented abundantly (and, to all appearances, pollinated largely) by certain minute insects which are of a kind no one can regard as intended by nature to pollinate them §.

How is this paradoxical result to be explained?

VII.—*Conclusion.*

From the foregoing, it becomes clear that, thus far, a satisfactory solution of the problem has not been reached. It is, therefore, necessary to search further for one. In so doing, one may well wonder whether the flowers of our Primulas may not be pollinated normally by some long-tongued insects which have not yet been detected in the act of visiting them.

This appears, indeed, to be the correct solution. There seems, in short, no alternative but to fall back on Darwin's hypothesis that pollination is

* Journ. of Botany, xxxv. (1897), p. 186.

† Essex Naturalist, v. (1891), p. 120.

‡ Nature Notes, xvi. (1905), p. 186.

§ That, in the Primrose, comparatively few of the flowers which bloom ever set seed is proved by even superficial observation. Mr. French doubts (Essex Nat. v. p. 120) whether as many as one *per cent.* do so. Mr. Highfield has observed (see Knowledge, xxxix. p. 115) that "only a small proportion of flowers on a plant, rarely exceeding half, sets its flowers." Yet that all the three species contrive somehow to secure pollination to some extent is certain; for all produce regularly an abundance of seed. This is more especially the case with the short-styled plants. Darwin showed long since ('Forms of Flowers,' pp. 17-20) that these are more prolific than the long-styled plants, and I have since demonstrated the fact on far fuller and more conclusive evidence (Trans. Essex Field Club, iii. 1884, pp. 168-169 and Tables V.-XV.). Yet, as I have also shown elsewhere (*op. cit.* pp. 157-163 and Tables I.-VI.), long-styled plants are in nature slightly more numerous than short-styled. Both facts may, perhaps, be connected in some way with the fact that, as shown herein, large quantities of pollen are regularly stolen from short-styled plants by predatory insects.

effected normally by night-flying moths*. Various considerations go to support this view.

In the first place, Darwin says† that one of his sons actually caught a moth, *Cucullia verbasci*, in the act of sucking a Cowslip flower—an interesting and, I believe, unique observation‡.

Secondly, the flowers of two of the Primulas under notice (namely, the Primrose and the Oxlip) are *pale yellow*—a colour which is exceptionally conspicuous by night and is characteristic of many flowers which are pollinated habitually by night-flying moths; whilst those of the third species (namely, the Cowslip, which probably depends more on the visits of day-flying insects) are of a deep yellow.

Thirdly, all three species possess nectar-guides (the five orange-brown spots forming the “eye” of the flower), and these are of a type usual in flowers pollinated habitually by night-flying insects—that is to say, prominent, but not sharply defined like the narrow lines seen on the petals of many day-pollinated flowers.

Fourthly, the scent of most, if not all, flowers which are pollinated habitually by night-flying moths becomes stronger after dusk—of course, to attract the moths which fly at that time; and this is the case with our Primulas‖. I was particularly struck with this fact on the evening of 22nd April, 1916, which was warm and still. About 6 o'clock, just as it was getting dark, I went into an old clay-pit, “carpeted” with Primroses in full flower, in a wood adjoining my garden, when I was struck at once and most forcibly by the strong scent of the Primroses, which permeated the whole atmosphere§. This it certainly does not do during the daytime, or to a very limited extent only; for the day-scent of all the three species is quite faint¶. On the other hand, it was probably the strong dusk-scent of the Primrose which attracted the numerous small creatures Mr. Dallman observed visiting the flowers after dark**.

* See *ante*, p. 107.

† Journ. Linn. Soc., Bot. x. (1869), p. 423, and ‘Forms of Flowers,’ p. 22 (see *ante*, pp. 108, 128).

‡ He omits to record whether the insect was caught during the day or the night, but says that he found on its proboscis an abundance of pollen of both forms. Sir Francis Darwin informs me that it was not he, but probably his brother, the late Sir George Darwin, an enthusiastic entomologist, who caught the insect.

§ Unfortunately, I omitted to observe *how long* the scent continued to be so strong. If to attract moths which fly only for a short time after dusk (as many do), probably it did not continue long.

‖ Prof. Boulger has said of the Primrose (Nature Notes, xv. (1904), p. 85) that it is “somewhat more scented, I think, at dusk or by night.”

¶ It is possible that the faintness of the day-scent of the Oxlip is accountable for the fact that many Continental botanists (e.g., Grenier & Godron, ‘Fl. de France,’ ii. 1850, p. 448) have described its flowers as scentless (“inodore”).

** Journ. of Botany, lix. (1921), pp. 320–322, &c. (see *ante*, p. 114).

There are yet other facts which have evidential value in this connection. It may be noted that, in the genus *Primula* (comprising, according to Pax & Knuth*, 208 species), a very large majority of the species have brightly-coloured flowers (usually red, pink, mauve, purple, or some combination of colours), while the very-small minority (certainly not 5 per cent. of the whole) have light-coloured flowers (white, whitish-yellow, or yellow). Further, it may be noted, that, of these few which have light-coloured flowers, nearly all are species which flower (unlike the majority) in early spring. These early-flowering species, eight in number, constitute a well-defined section of the genus (the "Sectio Vernales" of Pax & Knuth†), and all of these, with two exceptions, have yellow flowers‡. It is clear, therefore, that in this genus, yellow flowers and early-spring flowering are associated. Now, there can be no reasonable doubt that all the brightly-coloured species which flower during late spring and summer are pollinated by long-tongued humble-bees, butterflies, and other day-flying insects, for their comparatively-dark colour renders them very inconspicuous in the darkness of the night§.

These facts, then, go far to justify the assumption that the few exceptional members of the genus which have yellow flowers and flower in the early spring (which include the three species in question) are intended for pollination by night-flying insects; and there are (in Britain, at any rate) no such insects except moths.

Moreover, there is, indigenous to Britain, a considerable number of species of moth (chiefly hybernating species) which come abroad at the early season of the year when the three species of *Primula* concerned are in flower—say, roughly, from 15th March to 15th May. Dr. R. C. L. Perkins, F.R.S., has been good enough to prepare a list of some thirty-five species of Noctuidæ and Geometridæ which are known to do so. From this, I hoped I might be able to ascertain easily which species were those most likely to be concerned in the pollination of the flowers of our British Primulas. I soon found, however, that owing to the almost-complete lack of records of the tongue-lengths of British insects (already referred to ||), the list was of no help in this direction, inasmuch as there was not on it a single insect of which the tongue-length was known. In this dilemma, I received kind help from

* Primulacere (in Engler's 'Pflanzenreich,' vol. 22) (1905).

† *Op. cit.* pp. 47–65.

‡ They are *P. pseudo-elatior*, *elatior*, *leucophylla*, *acaulis*, *officinalis*, *heterochroma*, *amara* (purple) and *Julie* (red).

§ For instance, *P. farinosa*, a pink-flowered summer-flowering species, is known to be visited by insects very freely by day. Müller notes (*Fertil. of Flowers*, p. 386) no fewer than 48 species of Lepidoptera which visit it on the Alps, and a number of bees which visit it in North Germany.

|| See *ante*, p. 125.

Mr. W. H. T. Tams, F.E.S., of the British Museum, who kindly measured the tongue-lengths of most of the species on Dr. Perkins's list. The results were of much interest*. It appeared that, of nearly thirty species of moth of which Mr. Tams ascertained the tongue-lengths, *five species only* possessed tongues of sufficient length (say, 10 mm. or over) to reach the nectar in the flowers of any of the three *Primulas* concerned, namely:—

Calocampa exoleta (L.) (tongue-length about 12 mm.);

Calocampa vetusta Hub. (tongue-length about 12 mm.);

Phlogophora meticulosa (L.) (tongue-length about 11 mm.);

Cucullia verbasci (L.) (tongue-length about 20 mm.); and

Cucullia scrophulariæ Cap. (tongue-length about 20 mm.).

All these are common species and all have (like both the Primrose and the Cowslip) a natural range covering the whole of the British Isles. Finally, one of these five species (namely, *Cucullia verbasci*) is the only species which has ever been actually observed to visit a flower of any one of the three *Primulas* concerned†.

It is, therefore, beyond dispute that various species of moth capable of pollinating the flowers in question not only exist, but are common; also that one of those species has been taken in the very act of visiting a flower.

All the foregoing facts tend, I think, to show that Darwin's hypothesis, though as yet unproved, is probably correct. At all events, it has been accepted more or less definitely by I. H. Burkill‡, Lubbock§, E. G. Highfield||, and other writers on the subject.

That the Primrose *must* be pollinated in some places, at any rate, by moths solely seems clear from the fact that, on the remote island of St. Kilda, where the plant is "Plentiful on some of the cliffs,"¶ Mr. Alexander H. Gibson asserts** that "Butterflies, bees, wasps, and possibly ants, do not occur," though "several species of moths" (which he does not name) do occur; and he supposes (with, apparently, ample justification, assuming his facts to be correct) that, on the island, the Primrose and other flowers must be pollinated by these moths††.

The same may or may not be the case in Faroe, where, according to

* For details, see Journ. of Botany, lx. (1922), pp. 203–205.

† See *ante*, pp. 108, 128, 135.

‡ Journ. of Botany, xxxv. (1897), p. 186.

§ 'Brit. Flowering Plants,' p. 269 (1905).

|| Knowledge, xxxix. (1916), p. 113.

¶ See R. M. Barrington, in Journ. of Botany, xxiv. (1886), p. 215.

** See Trans. Bot. Soc. of Edinb. xix. (1893), p. 156.

†† Knuth quotes quite erroneously ('Flower Pollination,' iii. p. 69) this inference by Gibson, declaring that he attributes pollination to "flies"; and in this Knuth has misled at least one later English writer.

Ostenfeldt*, the Primrose has long been known to occur, and is apparently native, on rock-ledges near Trödun, on Sandö. Here, however, certain insects which might conceivably pollinate it are known to occur; for Neilsen says† that at least one species of bee (?*Bombus* sp.), a few Noctuidæ and Geometridæ, and a single individual of *Vanessa cardui* have been observed on the islands.

Yet, however probable—indeed, inevitable—this hypothesis may be, it is, for several reasons, very difficult to prove its truth conclusively. Thus, it is obviously far from easy—in fact, practically impossible—to follow closely in the dark the movements of any small flying creature; and, in the case of moths, there is the further difficulty that many of them fly at certain hours and for a short period (say, an hour or so) only. To make sure of seeing them at all, therefore, one must first ascertain the proper hour to watch, and then to watch at that particular hour; which is not always possible. Mr. Dallman, with the aid of an electric flash-lamp, was unable to detect any flying insect whatever in the act of visiting a Primrose‡.

It is for these reasons, probably, that Darwin's hypothesis on the point, though advanced as far back as sixty years ago and hotly discussed ever since, remains to this day neither proved nor disproved. Probably, indeed, it is quite incapable of absolute proof by means of ordinary observation. It ought, however, to be provable or disprovable, without great difficulty, by means of *direct experiment*; and I suggest that such be undertaken by some competent observer who happens to possess suitable opportunities.

There are two lines, along either or both of which (it seems to me) experiment might be carried out:—

First, some sticky substance, like bird-lime, might be placed in the evening in the bottom of the corolla-tube of a number of flowers, with a view to catching by the proboscis, and retaining till the morning, any insect which had visited the flowers during the night§. This method, if successful, would, of course, show the actual species of moth concerned.

Or, a number of plants (say, fifty or a hundred), all growing together in natural conditions (preferably in a wood), might be selected for experiment. Just before flowering, all might be "covered" (by the means usually adopted for preventing insects from obtaining access to and pollinating flowers) and so remain till all or most of the plants were in full flower. Then one half of

* 'Botany of the Faroes,' p. 50 (1901-8).

† *Op. cit.* p. 1066.

‡ Journ. of Botany, lix. (1921), p. 344.

§ I tried this with ordinary bird-lime as long ago as 1882, but with so little success (probably because I placed the bird-lime on the limb of the corolla, instead of in the tube) that I never repeated the attempt.

the plants might be exposed just after dusk and re-covered just before sunrise, while the other half might be exposed just before sunrise and re-covered just before dusk. This might be continued for (say) three days or nights, after which all the plants should remain covered permanently until the time when any seed they may have set should have ripened. If, then, the plants were examined and it was found that those which had been exposed by night only had fruited freely, while those exposed by day only had not, we should have good evidence that the plants are pollinated normally by night-flying moths; or, if the converse were found to be the case, we should know that the large-tongued bees and butterflies which are known to visit the flowers by day suffice to pollinate them adequately, though this appears at present to be impossible, owing to the fewness of their visits. But this method, though it might prove conclusively that the flowers are pollinated normally by night-flying moths, would not show the particular species by which this is effected.

For invaluable advice and help, I desire to thank many friends, most of whom have already been named; not least am I indebted to Dr. James Waterston, F.E.S., who has kindly identified the specimens in a small collection of bees taken by myself in the act of visiting *Primula* flowers, and Mr. Charles Nicholson, F.E.S., who has been good enough to read through my proofs.

29th August, 1922.

SPOLIA RUNIANA.—V. Summary of Results of Continuous Investigation of the Plankton of the Irish Sea during Fifteen Years. By Sir WILLIAM A. HERDMAN, C.B.E., F.R.S., F.L.S., Emeritus-Professor of Natural History in the University of Liverpool.

(PLATE 7 and 2 Text-figures.)

[Read 2nd March, 1922.]

INTRODUCTION.

THE history of this investigation, which has now extended over fifteen years (1907–21 inclusive), is briefly as follows:—After collecting and examining samples of marine plankton in a casual and sporadic manner for over quarter of a century on various parts of the British coast, in the winter of 1905 I became impressed with the view that the only hope of solving some of the problems of the plankton lay in a much more exhaustive study of a much greater number of samples taken as frequently as possible throughout the year at one locality, or series of localities, and extending over several years*. My connection with the Port Erin Biological Station and the staff at work there and in the Zoological Department of the University of Liverpool afforded the opportunity of organising a scheme of co-operative research, which later on became crystallised into six “official” hauls of the plankton net per week throughout the year, and a much greater number of “special” hauls (often ten or a dozen per day at sea, and amounting to as many as 36 hauls, in a small area two miles in extent, on one occasion) during certain critical months of the year (March, April, July, August, and September) when the plankton was specially abundant or was rapidly changing in character. The “official” gatherings were taken by the staff of the Biological Station inside Port Erin bay and consisted on each occasion of two horizontal surface-hauls across the middle of the bay, about half a mile, and one vertical haul, from 6 fathoms, close to the buoy at the entrance. The “special” hauls were taken by myself from a steamer both inside Port Erin bay and also at fixed “stations” in the open sea at distances of 3, 5, and 10 miles from land, with occasional days in the deep water (60 to 70 fathoms) halfway from the Isle of Man to Ireland.

For these purposes, during the summer of 1906, I chartered the steam-launch ‘Madge,’ and used her for a preliminary survey of the ground and

* The research has, however, extended over a much longer period than was at first contemplated, but new developments in the work kept opening up, and the value of cumulative evidence was impressed upon me. It was felt necessary to have thousands of samples to deal with and a number of years to compare.

the methods*. I then found that for facility of working and efficiency it was desirable to have a vessel and crew devoted specially to the work and on board which one could live and make more extended cruises, and keep all the necessary apparatus, &c., for working various kinds of nets and for preserving and examining collections. So from 1907 to 1914 (inclusive) the investigations were carried on from the steam-yachts 'Ladybird' (1907-10) and 'Runa' (1911-14)—especially the latter larger boat, in which with the most efficient help of the skipper Mr. James Crebbin we had the necessary gear for sounding, dredging, trawling, tow-netting, and the working of various special nets, water-bottles, &c., arranged so as to work smoothly and rapidly. During and since the years of war such continuation of the work as was found possible has been carried on from the 27-foot cutter motor-boat 'Redwing.'

In the case of most of these special collections taken from my own boats I was able to make a hurried microscopic examination of a sample from each haul in the living condition, and take a few notes of the nature and quantity of the gathering and of the prevalent organisms. In all cases, both "official" and "special," the gatherings (except when for safety they had to be preserved on board the yacht) were dealt with, fixed, bottled, and labelled by Mr. H. C. Chadwick, A.L.S., at the Port Erin Biological Station. The collections were subsequently worked over microscopically by Mr. Andrew Scott, A.L.S., and the numbers of each organism identified were counted or estimated and entered on our printed tabular forms, which were then sent to me for analysis and comparison with the other weeks, months, and years of the accumulating series. In all this work at Liverpool I had much help from my then secretary, Miss H. M. Lewis, B.A., who supplied me with the totals and averages I required, and drew up tables and graphs under my direction.

The results of each year were published annually in the Reports of the Lancashire Sea-Fisheries Laboratory at the University of Liverpool† for the years 1907-1921; but, for the most part, general results and conclusions were postponed until the completion of the series. Now that I have retired from active work at the University and the direction of the Port Erin Station, and have handed over the collection of upwards of 7500 plankton samples, and a corresponding number of tabular records, to the Department of Oceanography—where no doubt, in the hands of Prof. Johnstone, they will undergo further analysis and, I hope, yield good results,—it may be of some interest to those who are conducting plankton research elsewhere that I should give without further delay a brief summary of our records and some account of the conclusions at which I have arrived as the result of the fifteen years' "intensive" work.

* The results of that work in 1906 are not included in this survey of fifteen years.

† Trans. Biol. Soc. Liverpool, vols. xxii.-xxxv.

OBJECTS AND METHODS.

The objects of the investigation were stated in the first Report (1907) to be :—(1) to study the distribution of the plankton as a whole and of its various constituents during the year, and (2) to arrive at some estimate of the representative value of the samples collected in the plankton nets. Other problems were taken up from time to time, but these two remained the chief objects during the whole investigation; the results obtained in regard to them will be the main points discussed in this paper.

During the years preceding this work much attention had been directed, mainly as the result of the elaborate quantitative investigations of the Kiel School of Planktologists and the German Plankton Expedition in the Atlantic in 1889, to the supposed uniform distribution of the plankton organisms in sea areas under constant conditions; far-reaching conclusions were arrived at in regard to the amount of food-matters in the sea, and the numbers of floating fish-eggs and of the fish-populations—all based upon the assumptions of a uniform distribution over wide areas and of the validity of a comparatively small number of samples taken at considerable distances apart. Therefore it became obvious that a fundamental point in the investigation was to determine, if possible, the catching power of various nets, not in the laboratory, but under working conditions at sea, and to make comparisons between the catches of two exactly similar nets worked simultaneously and also successively at short intervals apart in space and time.

It is impossible to determine exactly how much water is strained by a net towed behind a ship. Even in traversing a measured distance at a known rate of towing with a net which has been measured and tested in the laboratory, there remain many other factors of unknown effect—such as uncalculated currents in the water and irregular movements of the boat, and also the unknown degree of clogging of the meshes according to the amount and nature of the organisms caught*—which prevent accurate conclusions being drawn as to the number of diatoms, &c., per gallon of water or per area of sea-surface. But we can compare two hauls of the same net taken in rapid succession, or the hauls of two precisely similar nets towed side by side over the stern, or again one at each side of the ship; or one may compare dissimilar nets and find one is consistently more effective than another either in the size of the catch or in catching some special type of organism. All these and many other experiments have been tried at Port Erin, and tried over and over again, and the results are recorded on our tabular forms; and although I do not attach importance to minor details†, still the wide

* See also W. E. Allen, of the Scripps Institution, California, on the same subject, in 'Ecology,' vol. ii. July 1921, p. 216.

† For example, when diatoms are present in millions per haul it is only millions that matter, and when Copepoda are present in thousands I pay no attention to the odd hundreds.

differences between the catches give, I believe, approximate results which are of value. When a number of similar hauls agree in their evidence, we must conclude that they are representative and give an approximation to a true picture of the contents of the sea at that place and time. When they differ widely we must, I think, be convinced that the plankton is very irregularly distributed and that therefore generalisations as to that sea-area must not be based upon any one or a few hauls.

In drawing any conclusions as to uniformity of distribution it is not sufficient to find that two or more nets agree in the quantity of their catch. The quality must also be considered, and it is by no means always the two simultaneous hauls that are most alike in bulk that agree best in the kind and number of contained organisms. For example, on April 13th, 1907, two similar surface nets, "B" and "C," towed together contained the one 16 c.cm. and the other 15.5 c.cm., but these were made up very differently in the two cases. In C there were no *Balanus nauplii* and no immature Copepoda, while thousands of both were present in B. Then again in B there were very few adult *Temora*, while in C there were over 4000, B had 650 larval Polychætes and C had none, B had 2000 *Oikopleura* and C only 150, and so on*.

During the diatom maximum, when the sea is swarming with these organisms, there is greater uniformity in adjacent hauls than at other times when a zooplankton is present, but even then the simultaneous hauls of two similar nets, though of the same general type, commonly differ to the extent that one may be double or some small multiple of the other—showing that we get a good general picture of the plankton by such hauls, but that they are not representative in minute detail†.

For further details as to our nets and methods of use, and subsequent computations, reference must be made to the Annual Reports—and especially to the first three, for 1907–8–9 (*loc. cit.*).

DISTRIBUTION OF THE PLANKTON.

In regard to the first object of the investigation "the distribution of the plankton as a whole and of its various constituents throughout the year," I dealt in a former part of the present series‡ with the general distribution and the form of the annual curve for the total plankton, and in some detail with

* The full list of between 20 and 30 organisms for each net is given in our first Annual Report, for 1907.

† I find that W. E. Allen, in California, comes to much the same conclusions (*loc. cit.* p. 218). He adds, "Hundreds of samples approximately enumerated will give a much better idea of actual conditions in the sea than ten samples enumerated with excruciating care."

‡ "Spolia Runiana.—III. The Distribution of certain Diatoms and Copepoda throughout the Year in the Irish Sea." Journ. Linn. Soc., Zool. xxxiv. p. 95 (1918).

the two dominant groups, the Diatoms and the Copepoda, up to the end of 1916, and further observations have only confirmed what was then stated. The spring maximum of phytoplankton, starting in March when the sea has still a low temperature and increasing to a climax in April, May, or June, the diatom minimum at the height of summer in July or August, the secondary lesser maximum in autumn (generally September or October), very variable both in extent and in constituent organisms, and, finally, the winter minimum have been recorded for every year and need no further demonstration. I am now, however, in a position to show, in the following table, the variation, both in amount and date, over the whole series of 15 years, of the great spring maximum—by far the most striking feature of the annual plankton cycle; and, moreover, to state that in most years this phytoplankton rise in the curve can be resolved into two elevations, an earlier formed mainly by species of *Chaetoceras* and a later due to species of *Rhizosolenia*. There are also some further details in regard to the distribution in time throughout the year of various groups of the plankton that can now be added:—

TABLE I.

Year.	Pl. max.	M'th. aver.	Record c.c.	Diat. max.	Dino. max.	Copep. max.
1907.....	Apr.	21.5	51	Mar.	May	Oct.
08.....	May	11.3	23.5	May	June	Sept.
09.....	May	24	41	Apr.	May	Aug.
10.....	Apr.	63.3	129	Apr.	July	July
11.....	May	46	60.2	May	June	July
12.	Apr. & Ju.	37.5	64	June	May	June
13.....	May	40.1	72.2	May	July	July
14.....	May	34.8	88.5	May	May	Jy. & Sept.
15.....	May	63.5	116.5	May	June	Aug.
16.....	June	61.8	175	June	July	Sept.
17.....	May	77.6	176.5	May	Aug.	Aug.
18.....	May	85.8	158	May	July	Aug.
19.....	May	36	99	May	July	July
20.....	May	45.3	102	May	June	Sept.
21.....	May	40	140	May	June	June

Table I. shows, for each of the fifteen years (1) the month in which the maximum of the total plankton occurred, (2) the monthly average in cubic centimetres of the hauls taken in that month, (3) the record (the highest) haul of plankton in cubic centimetres, (4) the month of the Diatom maximum, (5) the month of the Dinoflagellate maximum, and (6) the month of the Copepod maximum for each year.

On analysing the annual curve of the total plankton into its three chief factors, the diatoms, the dinoflagellates, and the copepods are found to succeed one another in that order. For example, the diatom vernal maximum was in March in 1907, in April in 1909, and in May in 1908, the dinoflagellate maximum was about a month later in each case, and the copepod maximum is usually about a month (sometimes more) after that of the dinoflagellates. The autumnal maxima are less definite than the vernal. The copepod rise in September or October is the most marked, the diatom increase is usually much less evident than in spring and is less regular in its appearance, while the dinoflagellate elevation is still less constant.

The cause of all these seasonal changes is still very obscure, and they may be due to the interaction of several factors. In addition to the normal series of stages in the life-histories of the organisms throughout the year, one naturally turns to the meteorological conditions prevailing at the various seasons as being a cause of the increase or the diminution in numbers.

Series of hydrographic observations were taken from the yacht on many occasions by several fellow-workers, who kindly helped me in different years—especially W. J. Dakin, W. Riddell, G. H. Drew, and H. G. Jackson.

The water of the Irish Sea west of Port Erin may, on the whole, be regarded as a homothermal and homosaline mass. The temperatures in many vertical series showed a slight gradual cooling from the surface to the bottom at depths down to 60 fathoms, the difference on nearly all occasions being less than half a degree centigrade, and the few exceptions may be due simply to surface-heating by the sun. Such slight differences cannot be used as evidence for the inflow of bottom colder currents from outside, and probably have little influence upon the vertical distribution of the plankton. The surface-temperatures at the inshore stations are lower in winter and early spring and higher in summer and autumn than at the stations furthest from the shore, and this is probably due to the influence of the land winter and summer temperatures upon the adjacent water.

The salinities (determined by titrations of the chlorine, and conversion by means of Knudsen's tables) show a difference of only 0·05 per mille between surface and bottom water, except in the case of the deep water in mid-channel, over 60 fathoms, where the bottom water may be as high as 34·38 per mille when the surface at the same spot is 34·05 per mille. Probably these small differences in vertical salinities do not cause any great changes in the distribution of the plankton. Consequently the observed differences between surface and deeper gatherings must be due to other causes. The influence of heavy rain, of sunshine, and of the alternation of night and day probably produce greater changes in the vertical distribution of the plankton than the slight hydrographic differences we have recorded.

The oxygen determinations varied from 6·5 to 6·8 c.c. per litre of water at

the surface and from 6.3 to 6.7 c.c. at 20 fathoms, the deeper water showing in all cases less than the surface at the same station *.

More recently (1912-14), Prof. Benjamin Moore and others have shown that there are considerable variations in the alkalinity of the sea-water during the year, and that this periodic change corresponds roughly with the planktonic cycle, the connection between the two being due to the reduction in the amount of carbon dioxide present, caused by the metabolic processes of the diatoms and rendering the water more alkaline.

The more or less sudden disappearance of the spring diatoms after the maximum is difficult to explain, unless it be due to the increase in alkalinity in the water, which, according to Moore, is a result of the photosynthetic activity of the phytoplankton. Other contributory causes may be, as has been pointed out by Brandt and others, the exhaustion of necessary inorganic food-matters, such as nitrogen or phosphorus compounds or of silica. For example, in 1909 the diatom maximum came to an end suddenly between May 24th and 28th, and the rapid diminution in numbers was not accompanied by any recorded change in either temperature or salinity or in general weather conditions. Alkalinity records were not started till a couple of years later, but it may be that the disappearance of the diatoms is a purely vital phenomenon due to their own metabolic activity in changing the constitution of the sea-water in which they are living. Another possible factor is that the increase in solar energy which favours the phytoplankton rise in early spring has now passed the optimum for these organisms and may be harmful, but that also is part of their metabolic activity.

Although one may arrive at the general conclusion that variations in the amount of the plankton from year to year must be due ultimately to meteorological conditions either at the spot or elsewhere, either at the time or earlier, it is not easy to demonstrate the connection between cause and effect in detail. Records of temperature of sea and air, twice daily, and of sunshine and other weather conditions have been kept for many years at the Port Erin Biological Station, and during 1909 we took determinations of the sun-light with a "Wynne" actinometer on days when plankton was being collected from the yacht; and, although there may be no obvious relation between the weather conditions of the day and the plankton catch, it seems possible to correlate the plankton curves with the sunshine records of previous weeks or months. For example, in the Report for 1909 will be found the records in detail for three years, and curves for the monthly averages of 1908 and 1909, showing a close correspondence between the sunshine and the plankton and giving in both cases a maximum in May.

* For further details in regard to all the hydrographic observations, see Report III. for 1909.

The curve for the temperature of the sea during the same period, on the other hand, does not correspond, and shows very little rise while the plankton is on the increase. It is clear, for example, that change in temperature of the sea will not account for the sudden increase in the plankton which began on April 9th, after five days of increased sunshine. During the five days, April 5th to 9th, when the sunshine record increased from 12.5 seconds to 2 seconds (by the actinometer), the sea-temperature increased only from 7.07 to 7.9° C., and this was followed after a week by an eight-fold increase of the plankton (from 100,000 to 800,000 diatoms per haul).

In the spring of 1910 there were more days and more hours of sunshine recorded at Port Erin than in any of the previous years, and the diatom record was also a high one. January, February, and March have in 1910 over 20 more hours of sunshine than in 1909, and about 13 hours more than the average of the same period in the four preceding years. In short, the early months of 1910 had an unusual amount of sunshine, and so had those of 1907, and we find that in these two years there was a much greater phytoplankton maximum in April than was the case in the two intermediate years. As it is possible that it is the sun in March that has most effect upon the April phytoplankton, we may quote here from our records the hours of sun in March for the four years:—

	1907.	1908.	1909.	1910.
March sun.. . . .	113	83	77	100
Plankton maximum ...	April	May	May	April

The individual hauls in April in each of the four years are much higher in 1907 and 1910—in brief, the diatoms appeared in great abundance earlier in April in the two years when there had been most sunshine in March.

The differences between successive years may be very great in both the quantity and the constitution of the plankton. For example, in 1907 one haul of the Nansen vertical net on April 5th gave 17 million diatoms, of which 14 million were *Chatoceras contortum*; and two surface-nets on September 12th gave 13 and 16 millions of *Rhizosolenia semispina*. In the following year, however, both these diatoms were comparatively rare at the corresponding seasons (April and September). Again, *Chatoceras contortum* and *Thalassiosira nordenskiöldii*, which were mainly responsible for the spring maximum in 1907, were much less prominent in 1908; and *R. semispina*, which reached millions in Sept. 1907, was almost absent in Sept. 1908.

It may be worth while, therefore, to give the following table II., in which are shown, for the series of years, the approximate time of the diatom maximum, the character of the plankton when any dominant organism was present, the general weather conditions of the year (abstracted from the Reports of the Meteorological Office), and the lowest sea temperature in degrees Fahr. during March:—

TABLE II.

Year.	Diat. max.	Temp.	Char. of Plankton.	Gen. char. of weather.
1907	Mar.	41°	Thalassios. & Microcal.	Sunshine early spring.
08	May	43	Later than '07.	Snow in spring; sunshine.
09	Apr.	41	Like '08; more June Pl.	Dry, sunny spring.
10	Apr.	44	More Diatoms.	Sunny spr., dull summer.
11	May	42	Oceanic invasion.	Dry warm spr. & summer, much sunshine.
12	A. & Ju.	45	Earlier than '11, abundant.	Mild spr., cold wet summer.
13	May	44	Oc. invas.—Asterionella.	Wet spr., dry, calm summer.
14	May	45	Chaetoceras.	Temp. higher, sunshine.
15	May	43	No swarms.	Wet, stormy spr., cool yr.
16	June	40	Chaetoceras; Ceratium.	Cold spr., wet & dull year.
17	May	40	Diatoms high in spring, low in aut.	Cold spr., wet Aug., storms.
18 ..	May	42	Diatoms abundant, & early.	Dull mild spring; wet.
19 ..	May	42	Calanus scarce.	Cold wet spr., dry summer.
20	May	43	More Pl.; like '18.	Mild wet spr., dull summer.
21	May	45	Diatoms abundant, & early.	Dry & warm, sunshine.

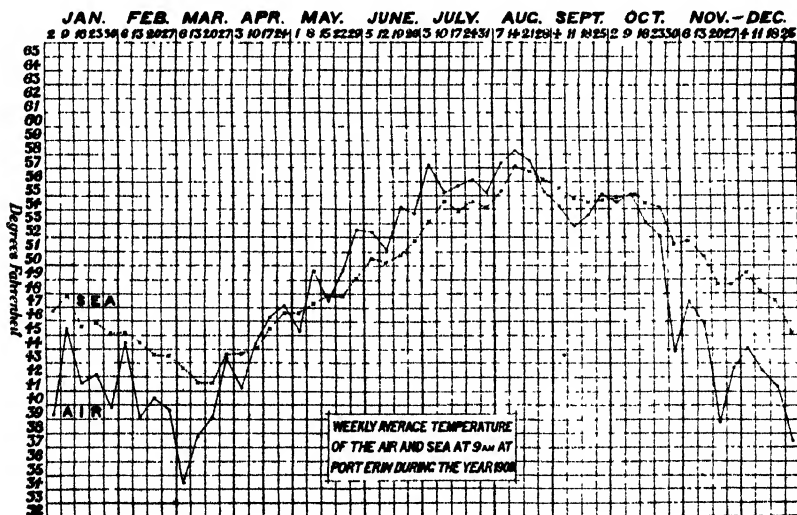


Diagram of Sea and Air temperatures at Port Erin.

As may be seen from this diagram of the sea and air temperatures at Port Erin during 1909 (and the various annual diagrams do not differ much) the sea temperature lags behind that of the air, and is generally as low, if not lower, in March, at the time when the phytoplankton is waking up to activity, as it is in January or February.

There is some evidence to show that the autumnal increase in plankton may be more closely dependent upon the weather of the moment than is the case with the spring maximum, and that, in fact, there is no very marked autumnal rise, unless the weather conditions are favourable. For example, in September 1907 a sudden increase in the phytoplankton coincided with the highest sea-temperatures of the year, and, at the same time, a week of fine calm weather with light easterly winds. Then, again, the summer of 1911 was exceptionally dry, warm, and sunny, while that of 1910 had been cold, gloomy, and stormy. August 1911 had 194 hours of sunshine recorded at Port Erin as against 80 hours in August 1910, and about 107 as the average for August of the previous four years; and any effect of this enormous increase in the August sunshine may naturally be looked for in the autumn and winter plankton, and possibly even in that of the following spring. We find, then, that the secondary diatom maximum in the late autumn of 1911 was unusually large. The numbers for the diatom monthly averages, per haul, in the two years are as follows:—

August	(1910)...	850	(1911)...	1,998
September	„ ...	676,823	„ ...	928,501
October	„ ...	553,601	„ ...	4,742,791
November	„ ...	100,262	„ ...	506,729

Thus, in 1911, the year of the remarkable August sunshine, the October phytoplankton was about nine times as great as in the previous year with the gloomy summer. Moreover, in the following spring (1912) diatoms made their appearance unusually early and in vast quantity. Nearly two millions per haul were reached on March 11th, and nearly 25 millions on March 21st, and these high numbers were kept up till the middle of June, the actual maximal haul being over 200 millions on May 30th; whereas in the spring of 1911 the millions were not reached till May 10th, and the numbers had dropped again by June 12th, the maximal haul being under 70 millions on May 16th. The Dinoflagellate maximum was in 1912 a month earlier than in 1911, and had on May 9th a haul of over 8 million *Peridinium*, the greatest number recorded in these series of investigations. Thus, the weather of the previous summer and autumn may have an effect upon the phytoplankton of the next spring and summer.

The contrast between a typical phytoplankton (diatoms and dinoflagellates) in late spring and a typical zooplankton in summer is shown well in the following record of the united monthly averages in the two cases:—

1911.	Phytoplankton.	Zooplankton.
May + June	28,046,330	98,333
July + Aug.	30,684	238,215

These are not the largest hauls, but only monthly averages, but the differences are quite sufficient to show the change in the nature of the predominant plankton in passing from the one period to the other.

In that year the spring maximum was in May, a single haul on May 16th giving over 60 c.cm. and containing over 54 million diatoms. The diatom maximum was in May, the dinoflagellate maximum in June, and the Copepod maximum in July.

At the time of a mixed plankton a sudden increase in the volume of the catch does not necessarily mean an increase in the number of the organisms prevalent at the time, or even an increase in the total number of organisms. For example :

	Diatoms.	Copepoda.
April 18th	4.5 c.cm.=238,000	and 7651
April 21st	22.5 c.cm.=194,000	and 2403

The rise in volume in this case was due to a comparatively small number of much larger organisms, such as medusæ, polychæte larvæ, fish eggs, etc. On the other hand, a sudden rise in the following month was due to an increase of the organisms prevalent at the time :—

May 4th	7 c.cm.= 115,450	diatoms.
May 10th	20.5 c.cm.=2,268,750	„

It is evident, then, that to draw conclusions merely from the quantity of the catch (in c.cm.) may be deceptive, and that it is necessary in all cases to make a microscopic qualitative examination, so as to ascertain the organisms that are present, and then estimate their approximate numbers.

DOMINANT ORGANISMS OF THE PLANKTON.

DIATOMS.

In "*Spolia Runiana*," III. (1918), I drew attention to the fact that the dominant organisms in the plankton which constitute the greater part of the summer zooplankton are about half-a-dozen species of Copepoda, and similarly in the case of the spring phytoplankton about the same number of genera of diatoms. These comparatively few species belonging to these two very different groups thus come to be the most significant organisms in relation to the annual metabolic cycle of our seas and the food-supply from our coastal fisheries.

Of the half-dozen generic groups of diatoms involved, the two most important genera in our seas are certainly *Chaetoceras* and *Rhizosolenia*. They are the only forms* that ever reach hundreds of millions per haul, and in 14 of the 15 years under consideration they are by far the most abundant organisms present in the plankton. Moreover, it is these two groups of diatoms that enable us to analyse the vernal maximum into two distinct elevations, the *Chaetoceras* rise being earlier (April-May) and the *Rhizosolenia* rise later (usually in June). It is therefore of some importance to consider the record of these two dominant genera throughout the series of years in more detail.

* With the exception of *Asterionella* in 1913.

Chaetoceras.

This is the most abundant and characteristic form of the spring (April and May) plankton in the Irish Sea. It is a large genus containing many species, of which at least a dozen have occurred in our gatherings off Port Erin, but it is only the following eight that attain to such numbers as to be really dominant constituents of the plankton, viz.: *C. boreale*, *C. contortum*, *C. criophilum*, *C. debile*, *C. decipiens*, *C. densum*, *C. sociale*, and *C. teres*. Of these, again, the most abundant species are *C. debile*, *C. decipiens*, *C. sociale*, and *C. teres*.

Some years seem to be much more favourable for the development of vast numbers of diatoms than others, some are good years for *Chaetoceras* but not for *Rhizosolenia*, and some are characterised by great abundance of one particular species. For example, 1907 was a poor year for both *Chaetoceras* and *Rhizosolenia*, 1912 was a good year for both, 1917 was a poor year for *Rhizosolenia*, but showed *Chaetoceras* in abundance. Again, *Chaetoceras sociale*, usually one of the most abundant species, was very poorly represented in 1918 and was practically absent in 1920, and *C. contortum*, present and prominent in most years up to 1915, was very scanty in 1918 and absent in 1919 and 1920. Consequently, from our statistics, we can speak not only of a "*Chaetoceras*" year and "*Rhizosolenia*" year, but also of 1909 being a "*teres*" year and of 1910 being a "*debile*" year, and so on—as the following statement will show in detail:—

Prevalence of *Chaetoceras* during 15 years*.

- 1907—A poor year, no millions per haul present at any time.
- 1908—April, a fair amount but no millions; May, *C. boreale* up to 1 million.
- 1909—April, *C. teres* up to 8 million.
- 1910—April, *C. debile* up to 24 mill. (on 22nd); May, *C. sociale* up to 15 mill.
- 1911—May, *C. debile* (30 mill.) and *C. sociale*; Sept., *C. debile*, *decipiens*, and *teres*.
- 1912—April, abundance of *C. sociale* (44 mill.), *debile* (36 mill.), *decipiens* and *teres* (16 mill., in March); Sept., *C. decipiens* (25 mill.).
- 1913—May, *C. debile*, but less than 1912.
- 1914—May, *C. debile* in large quantity (over 100 mill.).
- 1915—May, *C. debile*, *criophilum*, and *sociale* abundant.
- 1916—May, *C. sociale* (up to 23 mill.).
- 1917—April, abundance of *C. debile* (over 44 mill.) and *teres* (16 mill.); May, *debile* and *sociale* (30 mill.).
- 1918—May, *C. debile* (up to 38 mill.).
- 1919—April, *C. decipiens*; May, *debile*.
- 1920—May, *C. debile* and *decipiens*.
- 1921—Late April and early May, *C. debile*, *decipiens*, and *teres*.

Some of the species of *Chaetoceras* (*debile*, *decipiens*, *densum*, *contortum*, *criophilum*, and *teres*) begin to appear in small quantities quite early in the

* The months named are those in which diatoms of the genus *Chaetoceras* were most abundant in each of the 15 years; and when specific names are given they are the species which were most prominent in the plankton, and reached millions per haul at that time.

year, even in January and February, but do not attain to their maxima (millions per haul) until March, April, or even May. Other species, such as *boreale* and *sociale*, are later in appearing (April or May), and then usually reach the millions very rapidly. A few species (*boreale*, *debile*, *decipiens*, *densum*, and *teres*) may on occasions re-appear in September or even later in autumn, and under favourable circumstances run up rapidly to a secondary maximum.

The months in which the *Chatoceras* records are most numerous and reach the highest numbers per haul are March, April, May, and September, and of these the one with the greatest number of high records (in most cases millions) is May, the next being April, and then September.

The most barren months of the year, not merely for *Chatoceras* and *Rhizosolenia* but for records of diatoms in general, are November, December, January, February, and August. July would also be very poor were it not that the June maximum of *Rhizosolenia* (see below) on occasions extends into the beginning of July.

If we trace the prevalence of the five most abundant species of *Chatoceras* throughout the years, we find :—

<i>C. boreale</i>	has its maximum in May,	and again in Sept.
<i>C. debile</i>	„ „ April, May,	„ Sept.
<i>C. decipiens</i>	„ „ March, April,	„ Sept.
<i>C. sociale</i>	„ „ May.	
<i>C. teres</i>	„ „ April, May,	„ Sept.-Oct.

Rhizosolenia.

Out of the half-dozen species of *Rhizosolenia* that occur in the Irish Sea, there are only three that appear in our plankton gatherings in such abundance as to be of real importance, viz., *R. semispina*, *R. Shrubsolei*, and *R. Stolterfothi*, and of these the last-named is rarely (1913) as abundant as the other two. The months in which these three species occur are May, June, July, and occasionally again in September; but confining attention to the later spring or early summer phytoplankton maximum, which is clearly due to *Rhizosolenia*, the range of the three species mentioned is from the latter part of May through June and in some years into the early part of July. June is, then, the central month of this *Rhizosolenia* maximum, and June plankton gatherings are generally characterised by the dark-brown silky deposit which indicates the presence of *Rhizosolenia* in quantity.

Individual years may differ in being earlier or later, and also in the species which is present in greatest abundance—for example, 1908 and 1911 and '12 had the *Rhizosolenia* maximum early, in May and June; 1913 and '14 later, in June and July; while in 1919, '20, and '21 the *Rhizosolenia* maximum extended over parts of all three months. Moreover, the three

species succeed one another in the order—*semispina*, *Shrubsolii*, *Stolterfothi*. The May records are mostly of *semispina*, which does not occur so frequently in June and hardly ever in July. *R. Shrubsolii* is rare in the May gatherings, forms the greater part of those in June, and may also be abundant in early July. *R. Stolterfothi* only appears at the end of the *Rhizosolenia* maximum, late in June and early in July. In 1913 it was recorded in millions in July.

The following statement gives the distribution of these more prominent species through the different years, and shows that—as in the case of *Chaetoceras*—a species may be characteristic of a particular year, so that it is appropriate to speak of 1912 as a “*shrubsolii*” year, 1920 as a “*semispina*” year, and so on.

1907—Poor year, no millions, only *R. semispina* reached $\frac{1}{2}$ mill. (Sept.).

1908—Better; *semispina* and *Shrubsolii* both just reach millions (May and June).

1909—Poor year, only *semispina* abundant (June).

1910—Better; *semispina* (May); *Shrubsolii* every haul in June (=44 mill. in all, average over 6 mill.) and early July.

1911—Good; *semispina* abundant (late May and early June).

1912—A “*Shrubsolii*” year; both *semispina* and *Shrubsolii* reach millions late May and early June, but *Shrubsolii* the most abundant (about 100 mills. in several hauls), average for June over 40 mills.

1913—Shows succession: *semispina* early, then *Shrubsolii* abundant (June), then *Stolterfothi* (mills. July) after *Shrubsolii*.

1914—Only *Shrubsolii* (June and July).

1915—Another “*Shrubsolii*” year (June and early July), aver. for June=over 10 mills.

1916—Poor year, only *Shrubsolii* reached mill. once (July).

1917—Same as 1916.

1918—A “*semispina*” year, millions in May; *Shrubsolii* few.

1919—A “*Shrubsolii*” year, appeared unusually early and reached millions late in May, remained through June and into July.

1920—A “*semispina*” year, over 60 mills. late in May (average for May about 17 mills.), extends through June and part of July.

1921—A “*Shrubsolii*” year, begins late May, maximum middle June (over 8 mills.); *Stolterfothi* abundant end of June; *semispina* almost absent.

The only other genus of diatoms that sometimes approaches *Chaetoceras* and *Rhizosolenia* in numerical importance is *Thalassiosira*, of which two species occur in our Irish Sea plankton—*T. grävada* and *T. Nordenskiöldii*, and the latter is the more abundant. It may be regarded as a neritic northern species, and its occurrence in quantity in our seas can be taken as an indication that arctic water and northern plankton have invaded the British area. In April 1907 there was apparently such an invasion, and that spring *Thalassiosira Nordenskiöldii* along with *Chaetoceras contortum* and *C. debile* made up most of the diatom maximum. During the next few years the numbers of *Thalassiosira* were much lower, but it again appeared in quantity in 1912 (6 millions on April 29th) and 1913 (6½ millions on

May 16th), and in April 1915 and 1917 it was again abundant at Port Erin. In 1918, '19, '20, and '21 the maximum was early in May, but the numbers not high. In fact, it has only appeared in quantity in our gatherings in April and May, and not always then.

A few other prominent genera of diatoms are worthy of notice for one reason or another. *Coscinodiscus* is an early spring or even winter form, appearing along with *Biddulphia* while the water is still at its coldest and forming the first increase in the phytoplankton, generally in March but sometimes as early as February or even January. It is only very rarely that either *Coscinodiscus* or *Biddulphia* runs to millions per haul in our plankton, nor do they ever show the almost miraculously sudden increases that we see in the case of *Chetoceras* and *Rhizosolenia*; but they are individually large diatoms, and consequently "bulk large" in appearance in a plankton sample under the microscope. Though they occur at the same time of year they by no means flourish equally in the same year. For example, in 1912 the numbers for *Biddulphia* were considerably lower than those in 1911, and, on the other hand, the numbers for *Coscinodiscus* were higher in 1912 than in 1911. In 1919 *Biddulphia* attained to higher numbers in November than at the spring maximum—an exceptional occurrence.

Since 1909 two species or "forms" of *Biddulphia* have occurred commonly in the Irish Sea plankton—the commoner British *Biddulphia mobiliensis* (or *B. regia*, or "forma regia" of some) and the rarer, possibly exotic, species or form "*sinensis*." In my former paper* I discussed the curious history given by Ostenfeld of the spread of *B. sinensis* through the seas of North-West Europe since its appearance at the mouth of the Elbe in 1893; and in our Sixth Annual Report† we gave a plate showing variation in *Biddulphia*, from a series of photo-micrographs by Mr. A. Scott, which I repeat here in order to add the comments which Prof. Ostenfeld has sent to me in a letter. As recorded in our previous report, in 1911 and 1912 we noticed some specimens of *B. sinensis* which showed the normal characters of that form at one end of the cell, while the other end had the appearance of *B. regia*. The structure of these abnormal forms, which have continued to appear from time to time, is shown by figs. 5, 7, 8, 9, 10, 12, 14, and 15 on the Plate (Pl. 7). All these figures show clearly that one end of the cell is *Biddulphia sinensis*, while the other end shows a decided approach to the appearance of *B. regia* or *mobiliensis*.

We took the view in our 1913 report that the "*sinensis*" form was not a distinct species, but a mutation of *B. mobiliensis* (or *regia*). Since then Prof. C. H. Ostenfeld, after examining a sample, has written to me as

* "*Spolia Rumiana*," III. 1918—*loc. cit.* p. 179.

† Trans. Biol. Soc. L'pool, vol. xxvii. (1913) p. 204.

follows:—"I must admit that I cannot find any transition from *B. sinensis* to *B. regia*, or vice versa. When I got your Report for 1912 and looked thoroughly at the photos of Pl. I., I got at once the impression that figs. 1-15 were all *B. sinensis*, figs. 16-19 *B. regia*. This impression has been verified by examination of the sample. I have seen specimens of *B. sinensis* with supernumerary spines, specimens resembling fig. 5, and a few specimens resembling figs. 7-9, but I have not seen any real transitional stage to *B. regia*, all the deviation being, in my opinion, only abnormal (teratological) stages of *B. sinensis*. It seems to me that while *B. regia* is vigorous and healthy in the Irish Sea, *B. sinensis* is disposed to producing anomalies, most probably because the conditions of life are in some way or other not favourable for its development. After having examined this sample I feel still as much convinced of the independence and stability of the species *B. sinensis* as I felt before."

The opinion of such a distinguished authority as Prof. Ostenfeld must have great weight, but it must be remembered when considering these abnormal forms of *Biddulphia* that other similar cases of apparent transitions between species are known amongst diatoms, such as that of the arctic *Rhizosolenia hebetata* and our common Atlantic form *R. semispina* discussed by Gran*.

The less prominent and less well-known diatoms *Lauderia borealis* and *Guinardia flaccida* occasionally appear in large numbers and reach millions for a short time. *Lauderia* occurs along with *Chatoceras* in late April or May and *Guinardia* along with *Rhizosolenia* in June, so they help to swell the earlier and the later crests respectively of the spring diatom curve. *Lauderia*, for example, amounted to over 20 millions on April 22nd, 1910, and to 12½ millions on April 29th, 1912; and *Guinardia* to 18 millions on May 30th, and nearly 23 millions on June 3rd, 1912.

Asterionella is another form which on rare occasions runs up to very high numbers. The species *A. Bleakeleyi* is frequently present in small quantities, but in 1913 *A. japonica* appeared in enormous numbers for quite a short period in the middle of May and reached 192 millions in one haul on May 16th. Two months before and two months later none were present.

DINOFLAGELLATA.

The Dinoflagellate maximum in summer usually follows that of the diatoms, but is not nearly such a marked increase. In the 15 years recorded it has ranged from May to August, but has most frequently been in July. Some years, such as 1908, '12, '18, and '20, have been much more favourable than the rest, and in 1907, '9, and '17 the dinoflagellates were rather poorly represented. The favourable years are not always (1908)

* See Murray and Hjort, 'The Depths of the Ocean,' p. 320.

those that are best for diatoms; but in 1912 both groups were especially strong.

The chief genera represented in our plankton are *Ceratium* (chiefly *C. Tripos*) and *Peridinium**—several species of each,—and as a rule *Ceratium* is the more abundant and the earlier in attaining high numbers; but in 1912 *Peridinium* reached far greater quantities than *Ceratium*. The maximum was on May 9th when one haul gave 8,650,000, the greatest number of *Peridinium* we have ever recorded during these investigations. *Peridinium* is to be regarded as an oceanic form, and this exceptional abundance in 1912 agrees with other evidence † that that year our western coasts showed an unusually large invasion of Atlantic organisms.

In 1914 there were two well-marked dinoflagellate maxima, an earlier in May and an exceptionally late one in November.

Ceratium Tripos shows records of from 300,000 to 600,000 per haul in July 1913, June 1915, July 1916, '18, '19, and June 1920. We may take as a final example of the numbers of this group the year 1921. The early summer proved favourable for dinoflagellates, with a maximum in late May and June. By March 24th (unusually early) *Ceratium Tripos* had reached 18,000 per haul, and in early April all the common dinoflagellates were in the thousands. On May 13th *C. Tripos* reached 40,000, and on June 13th and 16th about 100,000. Species of *Peridinium* at the same time in the middle of June reached 170,000, but had had an unusually early maximum of 300,000 on May 20th.

Ceratium Tripos, although sometimes regarded as an oceanic form, is present all the year round in the Irish Sea, and in some years (*e.g.*, 1918, '19, '20, &c.) the average of all hauls amounts to several thousands in every month, and during June to November runs into tens of thousands.

Two other species of *Ceratium*, *C. furca* and *C. jesus*, are also commonly present in Irish Sea plankton, and in the summer of 1921 *C. furca* was especially abundant at Port Erin and was in an unusually active condition, several specimens at once being commonly seen moving across the field of view when the freshly caught plankton was put under the microscope.

COPEPODA.

Next after the diatoms, the Copepoda are the most important group in the plankton of the Irish Sea from the point of view of economics and metabolism. The Copepoda, as a whole, are a summer and autumn group, and

* There has been some confusion between allied species in the records from our seas, so it is best to deal with them as a generic group.

† See Herdman and Riddell on "Plankton of the West Coast of Scotland," Trans. Biol. Soc. L'pool, vol. xxvii, 1913.

form a very important part of the food of migratory fishes such as the herring and mackerel, and of the younger stages of many if not most of the other edible fish.

Out of the six most abundant species of Copepoda dealt with in the former paper on plankton published by the Linnean Society ("Spolia Runiana," III. 1918), I shall now select two—the small but very abundant *Oithona helgolandica* and the much less numerous but far larger *Calanus finmarchicus*—for special examination over the series of years. There is no doubt that both are important food-matters in the sea. The average number, per haul, of *Oithona* is over 8000 and of *Calanus* about 260.

Oithona is the most generally abundant Copepod throughout the year in the Irish Sea, but the months when it is taken in greatest numbers are June to November (incl.), with the maximum generally in July. There may also be a second maximum in October or November.

Oithona had a run of four "strong" years, 1911 to '14 incl.; and of these '11 and '14 were the strongest, the largest single hauls being over 225,000 on July 18th, 1911, and just under 200,000 on November 9th, 1914. There was another record year in 1919 when the maximum was unusually early (June–July) and the largest of any year in the series, averaging about 100,000 per haul for two months—100,100 on June 2nd and 115,280 on July 31st. The poorest years have been the first three (1907–'9) and, more recently, 1916 and '17.

Calanus finmarchicus is a northern oceanic form, and its centre of distribution seems to be the North Atlantic to the south of Iceland. Although a few specimens are to be found in the plankton hauls all the year round in the Irish Sea, whenever large numbers appear suddenly, as they commonly do in summer or autumn, that may be taken as an indication of an invasion of oceanic water with some of its contained plankton.

Apart from these periodic invasions, which are generally in July or early August, the highest numbers between May and October are generally between 1000 and 4000. When the numbers suddenly run up to 20,000 or 50,000 the cause is an invading swarm which has appeared, and which generally disappears again in a few days. In 1909 we have evidence of an unusually large swarm that entered Port Erin bay on July 17th and 19th, when hauls estimated at 20,000 each were obtained, while the official gatherings taken on July 15th and 21st gave no evidence of unusual numbers. Then, again, on July 11th, 1916, a swarm of *Calanus* appeared in the bay, when over 12,000 specimens were taken in one net, while a few days before a similar haul gave only 10 specimens and another a few days after gave only 200—the swarm was rapidly disappearing. An unusually high and unusually early record was 50,720 on May 17th, 1912. There is evidence of other less-marked swarms on July 4th and 18th, 1911.

The poorest years in the *Calanus* record are 1917, with a maximum of only 1440 on July 19th, and 1919, when the top number was 1240 on June 5th.

The swarms of *Calanus* are generally accompanied by local mackerel or herring fisheries*.

Microcalanus pusillus, first described by G. O. Sars in 1903, is a northern, deep-water, and very small species, which is found off the west coast of Norway only in depths over 150 fathoms (Sars) and in quantity to the north of Iceland in deep hauls (Paulsen). It appeared suddenly in numbers in our deeper gatherings from mid-channel in the autumn of 1907 (2500 on Sept. 12th), and has been present many times since. In 1921, for example, over 20,000 were taken in a haul at the mouth of the bay on March 28th, and again, in December 1918, there was a decided invasion of Port Erin bay by this deep-water Copepod.

When this minute species was first recognised by Mr. Andrew Scott in 1907 we supposed that it was probably another case of an invasion of the Irish Sea from the north, especially as in that year a northern diatom, *Thalassiosira Nordenskiöldii*, was present in great quantity; but it has been present in our records in very irregular numbers nearly every year since, generally with its maximum in winter or early spring. Even if not an invader from outside the Irish Sea, it is at any rate a deeper-water form which only occasionally spreads to the surface and the inshore shallow waters, and varies much in its occurrence from year to year.

MOLLUSCAN LARVÆ.

Lamellibranch larvæ are frequently present in the plankton in large numbers, and it is probable that they come from the large scallop bed (*Pecten opercularis* and other species) which lies within a couple of miles to the north of Port Erin at a depth of 20 fathoms. In view of the fact that some years are known to be much more favourable than others for the deposit and further development of molluscan spat, it is important to examine the variations in abundance of those larvæ during the 15 years.

In each successive year we find that the swarms of Lamellibranch larvæ are most numerous in the early months (January to May) and again in autumn (from September to November), their minimum being in the height of summer (July and August). Our largest spring records are 112,000 per haul in March 1919, 130,000 in April 1918, and 117,000 in April 1909. The autumnal records are never so high, averaging about 35,000, and rising to 56,000 in October 1912. On the whole, taking both spring and autumn

* See "Spolia Runiana," III. p. 193.

into consideration, the poorest years in the series are 1913, '14, and '16, and the most favourable for Lamellibranch larvæ 1918 and '19.

Gastropod larvæ are never present in our gatherings in such quantity as the Lamellibranchs, and their general distribution throughout the year is much the same.

OCEANIC AND NERITIC SPECIES.

During certain of the years (especially 1909 and '10) we made a careful analysis of the species which are commonly supposed to be of "oceanic" and "neritic" origin, with the view of ascertaining to what extent outside influence affected the plankton of the Irish Sea. Oceanic species* are those "holoplanktonic" forms which typically inhabit the open ocean, although they may also be found in coastal waters, and which have no fixed or resting bottom stages in their life-history. Neritic species are those typically found in coastal and comparatively shallow waters. Most of them have fixed or resting bottom stages in their life-history, and so belong to the meroplankton, but some neritic forms are holoplanktonic, being permanently free.

In our third Annual Report†, there is a full discussion of the occurrence during the three preceding years of the oceanic and neritic species, leading to the general conclusion that the organisms of the Port Erin plankton are on the whole chiefly neritic, the percentage of oceanic forms ranging during the three years from 30 to 60 per cent. If the numbers of neritic occurrences be added up for each month, they show that mid-winter (December and January) and mid-summer (July) are more oceanic in character than the intervening months, and that April, May, and October are the most neritic. The oceanic forms, although not always the most abundant, constitute the more permanent element of the plankton, the meroplanktonic neritic forms showing periodic increases and reductions in accordance with the life-cycles of the organisms concerned.

REPRESENTATIVE NATURE OF PLANKTON HAULS AND SAMPLES.

In regard to the comparative value, or catching power, of different nets, our experiments showed that as a deep-water net for vertical hauls the "Nansen" was much more convenient, reliable, and effective for work at sea, and especially in rough weather, than the "Hensen."

The "Shear-net" (the Heligoland "Sherbrutnetz"), with one square metre

* There are, however, some holoplanktonic forms (such as *Sagitta*) which seem to be equally at home in the open ocean and the coastal waters all the year round, and which may be called "panthalassic." Their presence along with neritic species cannot be taken to indicate any inflow of oceanic water.

† Trans. Biol. Soc. L'pool, vol. xxiv. 1910, p. 245.

of mouth and a shearing plate of the same size, made of coarse meshed canvas, is very effective for towing horizontally at various depths, such as 5 or 10 fathoms, in order to catch the larger organisms of the macroplankton such as *Sagitta*, the larger Crustacean larvæ, medusæ, and young fishes, and its catching power may be estimated at about 10 times that of our standard horizontal tow-nets of 14 inches diameter of mouth. Of these standard tow-nets, those made of No. 20 (now No. 25) Dufour's bolting silk caught more of the smaller forms of the plankton (microplankton), such as diatoms and dinoflagellates, and those made of the coarser No. 9 bolting cloth caught a larger number of the Copepoda and the larger larval forms and fewer of the small diatoms, and consequently in a zooplankton or a mixed plankton usually gave the larger catches. When, however, there was much microplankton in the water the finer-meshed net caught most.

One of the first objects of our experiments was to determine whether simultaneous hauls of two or more similar nets gave identical samples of the plankton, and as the result of many observations, under various conditions, year after year, the evidence was that they do not. Even when alike in quantity, the samples are generally unlike in quality, as we have shown above. These observations lead to the conclusion that the plankton is not evenly distributed through the water, but is in most cases disposed in zones, tracts, or swarms according to the nature of the organisms. This is especially the case with Copepoda and the larval stages of the higher Crustacea, *Sagitta*, *Tomopteris*, Medusæ, and other forms with some slight power of locomotion which may enable them to get out of one zone or tract of water into another. We have recorded various instances showing that Copepoda and other larger animals of the plankton are very markedly in swarms.

The phytoplankton is more evenly distributed, but even diatoms are usually more abundant in some zones of the water than in others. As a rule, during daylight the most abundant plankton of all kinds is found a few fathoms below the surface—say, from 5 to 10 fathoms. Our "weight" net, which was exactly the same as the surface-nets with the addition of a heavy weight attached to the rope so as to cause the net to tow some fathoms deep, invariably caught more than the nets above, and in many cases obtained about double the quantity of some organisms.

One of the difficulties in working the open-mouthed tow-net is that it is almost impossible to go fast enough to keep the net working near the surface and at the same time slow enough to prevent the water from "banking-up" in front, causing currents across the mouth. Consequently we found it necessary to prolong the mouth of the net into a funnel of canvas with the narrow end forwards so as greatly to reduce the amount of water entering the mouth. Another useful device we adopted, in order to avoid any possible

disturbance of the plankton in the wake of the ship, was to attach the two surface-nets to otter-board, which were run out one to starboard and one to port well forward so as to tow the nets in untouched water*.

VARIATION IN SUCCESSIVE VERTICAL HAULS.

A few experiments have been made in the past, by Hensen and others, in hauling comparable nets simultaneously or the same net several times in rapid succession, in order to estimate the amount of variation in the results or the divergence of each sample from an average. With the view of getting further evidence from a new series of data, taken with all possible care under favourable conditions, I carried out a number of similar experiments at Port Erin during several months in the spring, summer, and autumn of 1920. They consisted of seven series of four to six successive (that is, as nearly as possible simultaneous) vertical hauls taken with the "Nansen" net of No. 20 silk†.

An apparent uniformity in the successive catches of each series was obvious at the time of collecting. It seemed to the eye to be the same catch that was emptied from the Nansen bucket into the bottle of formaline time after time throughout a series. And this apparent uniformity of volume was in most cases confirmed by the measurements in the laboratory—for example, the six successive hauls from 8 fathoms on April 3rd all measure 0·2 c.c., four out of five of those from 20 fathoms on April 6th are 0·6 c.c., and all four on August 7th from 20 fathoms measure 0·5 c.c. The remaining four series show some variation, but the percentage deviation from the average of each series is in no case great.

If, however, we make a microscopic investigation of the catches, we find that, even in the same series, similar volumes of the plankton may be made up rather differently, and may in some cases show surprising differences in the numbers of a species in successive hauls, such as 10 and 100, 40 and 800, 4000 and 18,000. Notwithstanding, then, some appearance of similarity between the hauls of a series, there is a considerable percentage deviation in the case of some hauls from the average of their series—not infrequently about plus or minus 50 per cent., and in several cases about 70 and in one case plus 129. The following table gives the percentage deviations in the case of the volumes of the catches, and also of the counted or estimated numbers of the four chief groups of organisms present, viz., Diatoms, Dinoflagellates, Copepoda, and the nauplii of Copepoda :—

* For further details in regard to these and other experiments see the Annual Reports, *loc. cit.*

† For full details as to the conditions of the experiment and the methods of obtaining the results here given, see Trans. Biol. Soc. L'pool, vol. xxxv. p. 161 (1921).

Date and Depth.	No. of hauls.	Vol. in c.c. average.	Greatest per cent. deviation from average.	Diatoms ditto.	Dinoflagellates ditto.	Copepoda ditto.	Copepod Nauplii.
April 3— 8 fathoms	6	0.2	0	$\begin{cases} -52 \\ +24 \end{cases}$	$\begin{cases} -42 \\ +24 \end{cases}$	$\begin{cases} -14 \\ +21 \end{cases}$	$\begin{cases} -19 \\ +39 \end{cases}$
April 6— 20 fathoms	5	0.58	$\begin{cases} -14 \\ +3 \end{cases}$	$\begin{cases} -51 \\ +41 \end{cases}$	$\begin{cases} -53 \\ +56 \end{cases}$	$\begin{cases} -50 \\ +42 \end{cases}$	$\begin{cases} -44 \\ +41 \end{cases}$
April 8— 20 fathoms	6	0.52	$\begin{cases} -23 \\ +15 \end{cases}$	$\begin{cases} -24 \\ +17 \end{cases}$	$\begin{cases} -20 \\ +15 \end{cases}$	$\begin{cases} -40 \\ +22 \end{cases}$	$\begin{cases} -39 \\ +22 \end{cases}$
April 13— 8 fathoms	5	0.48	$\begin{cases} -17 \\ +25 \end{cases}$	$\begin{cases} -41 \\ +73 \end{cases}$	$\begin{cases} -65 \\ +44 \end{cases}$	$\begin{cases} -22 \\ +33 \end{cases}$	$\begin{cases} -57 \\ +129 \end{cases}$
May 25— 20 fathoms	4	16.125	$\begin{cases} -10 \\ +21 \end{cases}$	$\begin{cases} -21 \\ +15 \end{cases}$	$\begin{cases} -22 \\ +23 \end{cases}$	$\begin{cases} -72 \\ +60 \end{cases}$	$\begin{cases} -33 \\ +56 \end{cases}$
August 7— 20 fathoms	4	0.5	0	$\begin{cases} -70 \\ +59 \end{cases}$	$\begin{cases} -27 \\ +17 \end{cases}$	$\begin{cases} -13 \\ +32 \end{cases}$	$\begin{cases} -21 \\ +10 \end{cases}$
September 16 20 fathoms	4	6.1	$\begin{cases} -26 \\ +23 \end{cases}$	$\begin{cases} -36 \\ +30 \end{cases}$	$\begin{cases} -22 \\ 36 \end{cases}$	$\begin{cases} -36 \\ +53 \end{cases}$	$\begin{cases} -31 \\ +37 \end{cases}$

In all there are about 50 species of organisms that occur with fair regularity throughout the series: 24 species of diatoms, 4 of dinoflagellates, 8 of Copepoda, and about 14 other organisms or groups of organisms which are not of so much importance and may be omitted. Of the 24 species of diatoms, as a general rule, if a species occurs in one of the hauls of a series it occurs in all, and in many cases in much the same proportions in all—that is, there may be two or three or even more times as many individual cells in one haul as in another, but all will be in the tens, or in the hundreds, or the thousands, or millions. For example, on April 3rd we have:—

Coscinodiscus radiatus, 1600, 2600, 2600, 2800, 2800, 2200.

Streptothecha thamensis, 40, 30, 40, 40, 60.

Many other similar examples might be given from the detailed records, but, on the other hand, other occasions show more variation. It is much the same with the four common species of dinoflagellates recorded. There, again, we find cases of considerable constancy in the hauls of a series, such as:—

May 25th—*Peridinium divergens*, 46000, 62000, 50000, 44000;

and other cases of more variation, even in that same series, such as:—

May 25th—*Ceratium furca*, 6000, 2000, 8000, 1000.

Are we entitled from this to conclude that the *Peridinium* is evenly distributed through the zone of water sampled and the *Ceratium* much less so? I doubt it.

The Copepoda seem also to indicate in many cases a fairly even distribution. Sometimes they occur only in units, and yet each haul of the series shows a few:—

April 3rd—*Oithona similis*, 8, 4, 3, 3, 5, 11;

April 13th—*Temora longicornis*, 10, 5, 10, 10, 10;

April 13th—*Oithona similis*, 20, 20, 20, 20, 20.

Other cases, again, seem to indicate considerable variation in adjacent hauls. Which of these contradictory impressions received from an inspection of the results of the hauls is true to nature? If the *Oithonas* on April 13th had been very irregularly scattered through the water, is it likely that we could catch exactly 20 in each of five successive hauls? On the other hand, if they are evenly distributed, how can we account for one haul (April 6th) catching 40 and the next 140, or for the series on May 25th—20, 80, 460, 290, in the four successive hauls?

Some of the other common organisms of the plankton outside the above main groups also give conflicting evidence. The pelagic arrow-worm, *Sagitta bipunctata*, is present in nearly every haul in numbers varying from one to twenty-seven, but in some series one or two individuals are present in every haul, while in another series the successive hauls varied from one to eleven. The impression one receives from an inspection of the lists and numbers as they stand is that if on each occasion one haul only in place of four or six had been taken, and one had used the results of that haul to estimate the abundance of any one organism or group of organisms in that sea-area, one might have arrived at conclusions about 50 per cent. wrong in either direction.

Is such a result of any real value as a basis for calculations as to the population of the sea? And is it possible that such numerical variations are compatible with the hypothesis of an even distribution of the plankton throughout a sea-area of constant character? The answer to such questions depends to some extent upon the possible range of error under the conditions of the experiment, and upon the possibility of allowing for that experimental error, and of reducing it by more refined methods of collecting and estimating. I feel confident that the possibility of error in the collecting was reduced to a minimum. There is also the possibility of error in the microscopic examination and estimation of the contents of the catch. This can only apply in the case of the more minute organisms, present in great abundance, such as the diatoms, which have to be estimated from counted samples. In the case of Copepoda and *Sagitta* and other larger organisms this source of possible error is excluded, as these are picked out from the

entire preserved catch with the eye or a hand-lens, and counted directly. Sampling and estimation are not applied to the macroplankton, and yet the variation is as great there as in the case of the estimated microplankton.

The experimental error to be expected in the case of the three chief groups of organisms, and also in the case of a typical species of each, has been calculated, by means of a formula for obtaining the probable error, with the following results.

The total number of diatoms on April 3rd varied in the six hauls from 3880 to 10,020, the mean being 8055. Two of the hauls are below the mean and four above. The smallest haul is 52 per cent. below the mean and the largest haul is 24 per cent. above. The question is—Do these variations in the catch come within the limits of the probable error of the experiment? If we assume that the estimation of the number of diatoms in each haul is correct, then the possible errors are those inseparable from all such collecting at sea—slight movements of the boat, unknown currents in the water, irregularities in the verticality of the line, &c. In this case of the diatoms on April 3rd the “probable error” is found to be = 1458, and the “range” is the mean \pm the probable error—that is, from 6600 to 9500. Comparing this range with the estimated results of the hauls, we find that three of the series are within the range and three are outside it, and two of the latter (3880 and 10,020) are very considerably beyond the limits of the probable error of the experiment.

The diatoms of the other hauls give much the same result when treated in the same manner—that is, roughly 50 per cent., or rather more of the observed variation in the catches is not covered by the calculated range of error of the experiment.

A series of detailed tables are given in the full report* from which the above is summarised, in which each of the principal groups of the plankton and also three prominent organisms—the diatom *Coscinodiscus radiatus*, the dinoflagellate *Ceratium tripos*, and the copepod *Pseudocalanus elongatus*—are shown for all seven series of hauls treated as in the case of the diatoms of April 3rd discussed above, and giving in each case the figures necessary to make a comparison between the range of variation in the catches and the calculated range of error. These tables show that in each case a large proportion—from 50 per cent. to 22 out of 34—of the observed variations are outside the range of error of the experiment.

To the question, What light does a series of, say, six successive hauls throw upon the validity of a single haul (say, the first of the series)?—the answer seems to be that as regards mere size (volume) and general nature (such as phytoplankton, zooplankton, or mixed) of the catch the series confirms the representative character of the single haul in a general way and within limits.

* Trans. Biol. Soc. L'pool, vol. xxxv. (*loc. cit.*).

But, if one next proceeds to deal quantitatively with the groups and the individual species, it is found that the hauls in a series may differ widely—up to fully 50 per cent. of the variations from the mean of the series extend beyond the range of error and are therefore not due to possible imperfections in the experiment. Thus more than half the differences between the hauls of a series remain unaccounted for, and may naturally be interpreted as evidence of an unequal distribution of the plankton in closely adjacent areas of water or in the same area in successive periods of time.

Whether the present methods of collecting and of estimating are sufficiently accurate to enable us to determine the amount of this inequality in the distribution, so as to be able to assign probable upper and lower limits to the number of each organism per unit volume of water, may be doubtful, but we may hope that improvements in method and accumulation of evidence may in time enable us to make some approximation to an estimate of the population of various sea-areas. Other more refined methods of collecting samples of the microplankton have been recently devised, such as the filtering and centrifuging (or other exhaustive examination) of small measured quantities of water, or the cultivation of every organism in a very small volume of water. These methods have added much to our knowledge of the minuter and more elusive forms of the plankton, but the drawback to all of them is that they deal with relatively small volumes (one, three, or five litres) of the water, and it must remain doubtful whether the same organisms in the same quantity would have been present in the next bucketful of water that might have been taken from the sea.

Even if we had no hope of attaining to greater accuracy, our present planktonic results are of some value. Although estimates which may be 50 per cent. wrong in either direction do not justify us in calculating exactly the number of organisms or of potential food present per area of sea or volume of water, they do give us a useful approximation*. Even if 100 per cent. out, doubling or halving the estimated number is a relatively small variation compared with the much larger increases and reductions, amounting to, it may be, ten thousand times in the case of diatoms, ten to fifty times in the dinoflagellates, and five to twenty times in Copepoda, which we find between adjacent months—and even greater differences if we take groups of months—in a survey of the seasonal variations of the plankton.

PHYTOPLANKTON IN RELATION TO FISH LARVÆ.

It has been stated above that it is only a very small number of kinds of organisms (plants and animals) that make up the bulk of the plankton that

* As W. E. Allen, of California, says:—"Tow-net catches give no trustworthy indication of the relative amounts of phytoplankton in two different locations or in the same location at two different times, although they may have a high suggestive value" ('Ecology,' ii., July 1921, p. 216).

is of real importance to fish. About half-a-dozen species of Copepoda constitute the greater part of the summer zooplankton suitable as food for larval or adult fishes, and about the same number of generic types of diatoms similarly make up the bulk of the available spring phytoplankton year after year. This fact gives great economic importance to the attempt to determine with as much precision as possible the times and conditions of occurrence of these dominant factors of the plankton in each year. An obvious extension of this investigation is an enquiry into the degree of coincidence between the times of appearance in the sea of the plankton organisms and of the young fish, and the effect of any marked want of co-relation in time and quantity.

Most of the food-fishes in our seas produce floating (pelagic) eggs which hatch out as larvæ in spring at periods varying from February to May, according to the kind of fish and the temperature of the water—a low temperature retarding the spawning and subsequent development. The marked increase in the number of diatoms in the water which causes the vernal plankton maximum begins to show at the very period when the fish larvæ are produced in greatest quantity, viz., March and April, in the Irish Sea. We have seen that the diatoms vary in their abundance and date of first appearance from year to year, and the question arises—Are they also, like the fish-larvæ, retarded in development by the low temperature, or the want of sun, in a late season, so that there comes to be some correspondence in date between the larvæ and the natural food upon which they are dependent after the absorption of their food-yolk?

Dr. Johan Hjort* has made the suggestion that if on occasions the larvæ are hatched out before their food is present in sufficient abundance, there may then be an enormous mortality of larvæ, which will affect the young fish-population of that year and greatly reduce the numbers of that particular "year-class" of that fish in the commercial fisheries of successive years for some time to come. So that, in fact, the numbers of a year-class may depend not so much upon a favourable spawning season as upon a coincidence between the hatching of the larvæ and the presence of abundance of phytoplankton† available as food.

In a general way, the curve for the spring maximum of pelagic fish eggs in the Irish Sea begins to rise late in February and remains high throughout March and April. The diatom curve also starts towards the end of February and usually remains high throughout March, April, May, and June. There is evidently a general correspondence between the two maxima, but is it sufficiently exact and constant to meet the needs of the case? The phytoplankton may still be relatively small in amount during February and

* Conseil Internat. Explor. de la Mer—Rapp. et Proc. Verb. xx., 1914.

† Including in "phytoplankton" the Flagellata and other minute organisms which may be present with the diatoms.

March in some years, and it is not easy to determine exactly when, in the open sea, the fish-eggs have hatched out in quantity and the larvæ have absorbed their food-yolk and started feeding on diatoms.

If, however, we take the case of one important fish, the plaice, we can get some data from our hatching experiments at the Port Erin Biological Station, which have now been carried on for about eighteen years. We have records for each year of the quantities dealt with and of the dates when the first fertilised eggs were seen, when the various batches of eggs were placed in the hatching boxes, and when the larvæ were taken out to sea. Consequently complete series of figures for the comparison of the dates for fish-larvæ and phytoplankton can be given for the series of years, and these show a certain amount of correspondence and also a certain amount of divergence.

We find that the dates for the first fertilised eggs range from the middle of January (1920) to March 3rd (1904). Excluding these two records as exceptional, we have a run of 15 consecutive years with dates ranging from February 5th to 26th, and the average date for the first fertilised plaice-eggs in the Port Erin spawning pond * is about February 20th. The dates when the first larvæ are set free in the sea have varied from Feb. 23rd (1914 and 1920) to April 10th (1904), and the usual date is about March 20th. The earliest date for the phytoplankton in the sea is Feb. 5th (1907) and the latest April 13th (1908). Omitting February and April, we have a run of ten consecutive years (1910 to 1919) when the dates range from March 4th to 22nd, and a central date for the beginning of the diatom increase may be taken as about the middle of March. A central date for the phytoplankton maximum in these years is about the middle of May.

It is evident, then, that in most of these years the diatoms were present in abundance in the sea a few days at least before the fish-larvæ from the hatchery were set free. Out of the 13 years (1907-1919) in nine cases (1907, 1910-12, and 1915-19) the phytoplankton preceded the appearance of the larvæ, and it was only in the remaining four years (1908, '09, '13, and '14) that there was apparently some risk of the larvæ finding no phytoplankton food, or very little.

The evidence, so far, seems to show that if the fish-larvæ are set free in the sea as late as March 20th they are fairly sure of finding suitable food; but if they are hatched as early as February they run some chance of being starved.

I had an opportunity at Port Erin during the hatching season of 1921 of examining the contents of the alimentary canal in a number of living larval and early post-larval plaice, and found:—(1) that it consisted of algal spores,

* For further details in regard to the conditions of this experiment at Port Erin, see the Annual Report for 1920.

diatoms, and green and brown disintegrated material which was doubtless of phytoplanktonic origin, along with occasional small copepods (in one case I was able to watch through the transparent walls of a young, living, post-larva the passage of the remains of a copepod along the intestine until it was extruded along with other material as a faecal pellet); and (2) that the larvæ began to take in solid food before the contents of the yolk-sac had been completely absorbed.

CONCLUSIONS.

The following conclusions may safely be arrived at from our statistics:—

In reviewing the records of this run of 15 years (1907–1921) we find that the spring phytoplankton maximum may range from March to June, and is chiefly composed of diatoms which vary from year to year in maximum haul from under one million in 1907 to about 206 millions in 1913.

This immense diatom elevation can be resolved into an earlier crest in April or May, chiefly formed of *Chaetoceras*, and a later in June, chiefly formed of *Rhizosolenia*.

The dinoflagellate maximum follows about a month later than the diatoms, and varies in our records from May to July (rarely August).

The copepod maximum is later again, and ranges from June to October.

Any one of these three main groups of the plankton or all of them may have secondary less conspicuous maxima in late summer or autumn ranging from September to November. Rarely, an autumnal maximum may, under favourable conditions, attain to large dimensions—for example, in 1912.

During the time of the diatom maximum in spring the organisms are more evenly distributed over the sea and downwards through the layers than is the case at other times of year and in the case of other larger organisms.

As a general rule, with a mixed plankton or a zooplankton, in the daytime the largest hauls are obtained not at the surface but a few fathoms below, round about 5 fathoms. The precise depth on each occasion probably depends upon the meteorological conditions and especially the amount of sun-light. Most marine organisms, perhaps all, seem to find their optimum of sun-light not in the maximum at the surface but in some degree of twilight conditions lower down.

In spring (April, May, or June) the gathering obtained from the tow-net is usually a "monotonic phytoplankton" (mainly diatoms), and in summer (say, August) it is frequently a "monotonic zooplankton" (Copepoda). On other occasions it is a "mixed plankton," and may contain large quantities of larval stages of coastal animals—such as Echinoderms and molluscs.

Taking the year round, the Irish Sea plankton is a mixture of "oceanic" and "neritic" organisms, roughly 50 per cent. of each, or rather more of neritic forms, the oceanic ranging from 30 to 60 per cent. Mid-winter and mid-summer are more oceanic in character than the intervening months.

A comparatively small number of genera of Diatoms and Copepoda, half-a-dozen of each, are the dominant organisms of the plankton, and make up by far the greater part of the phytoplankton and zooplankton respectively, and these are the all-important organisms upon which the nutrition of higher animals and ultimately of the food-fishes from the sea depends.

It is possible, moreover (as suggested by Hjort), that the survival of large numbers of newly hatched food-fishes in early spring, upon which will depend the prosperity of commercial fisheries a few years later, is determined by the amount of phytoplankton present at that particular time in the sea.

It seems probable that the vernal increase in phytoplankton, one of the great phenomena of the ocean, depends primarily upon the rapid increase in the amount of solar energy which accompanies the lengthening days of early spring, especially about the time of the vernal equinox. Thus, general meteorological conditions are linked up with the commercial fisheries of several years ahead. The diatom maximum in spring is no doubt aided by the winter increase of carbon dioxide and other food-matters in the sea. The rapid disappearance of the diatoms after the maximum may be due to some toxic effect upon the water caused by their own metabolism in dense crowds.

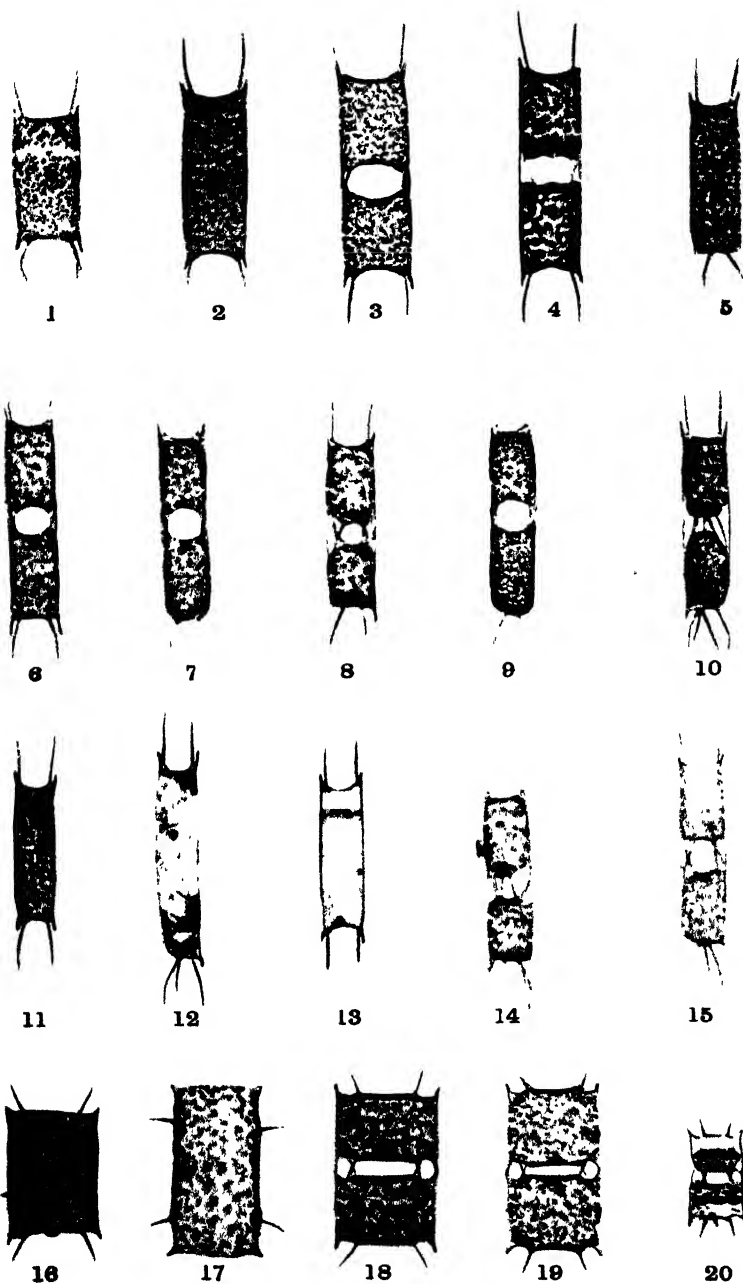
It is impossible to draw numerical conclusions as to the population of large sea-areas from few and small samples of the plankton.

Even series of vertical hauls taken at the same spot in rapid succession show so much variation from their mean that conclusions drawn from any one haul might be anything up to 50 per cent. wrong in either direction.

We arrive, then, at the conclusion that the distribution of plankton in the sea is not uniform, and that many animals such as Copepoda are present in swarms or patches.

EXPLANATION OF PLATE 7.

Variations of *Biddulphia sinensis* and *B. regia* in the Irish Sea. From photo-micrographs by Mr. Andrew Scott. (For detailed explanation, see pp. 155 & 156.)



VARIATION IN BIDDULPHIA.

Photo by A. Scott.

Critical Studies of Coal-measure Plant-impressions*. By the late E. A. NEWELL ARBER, M.A., Sc.D., F.G.S., F.L.S., Trinity College, Cambridge, University Demonstrator in Palaeobotany.

(PLATES 8-15 and 2 Text-figures.)

[Read 15th June, 1922.]

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I. A Revision of the British Upper Carboniferous Species of the Genus *LEPIDOSTROBUS*, Brongn., preserved as incrustations.

INTRODUCTION.

THE genus *Lepidostrobus*, instituted by Brongniart in 1828 for a particular type of Lycopod cone common in the Coal Measures, is one of the most stereotyped organs known from the rocks of this period. Its general structure, as evidenced both by petrifications and impressions, is too well understood to need description here. One of the chief features of this cone, however, is the very small range in variation met with, excluding factors of such doubtful value as mere size and shape. For this reason the discrimination of species has always been a difficult matter, especially in the case of incrustations. Among petrified specimens it is known that there is, as a rule, great uniformity in type, though Mr. Maslen (21. p. 357) and, at a later date, my wife (1. p. 205) have shown that certain variations do occur, some of which are probably of sufficient importance to be regarded as of specific rank.

* [Owing to the death of the Author before these studies were finally revised, I am responsible for their present form. I have to acknowledge a grant from the Royal Society in aid of the preparation of this and other memoirs left by my husband in various stages of completion. The Cannock Chase Colliery Company have also been kind enough to contribute £10 towards the cost of the illustrations. I am indebted to the Keeper of the Geological Department of the British Museum (Nat. Hist.) and to Prof. Boulton of the University of Birmingham, for the opportunity of studying specimens in their charge. I wish, also, to express my gratitude to Prof. J. E. Marr, F.R.S., who has given me every facility for work in the Sedgwick Museum, Cambridge, where most of the specimens illustrated in this memoir will be found.—AGNES ARBER.]

These remarks apply in particular to those cones which have comparatively undifferentiated sporophylls, the standard of comparison here as regards differentiation being the leaf. In dealing with impressions of such cones it is, of course, quite impossible to recognise those characters which in the case of petrifications are regarded as of taxonomic value. Such, in fact, are only visible under the microscope. For these reasons the classification of impressions of *Lepidostrobi* has always been a difficult matter, and authorities have differed as to the species which should be recognised, and as to their essential characters.

A desire for more definite progress in this respect has, indeed, been felt from quite early times. As far back as 1838, Brongniart (3. ii. pl. 12) illustrated the range of sporophyll-form met with among the living Lycopods, to serve as a basis for such studies, and the analogy has also been pointed out by others since. I do not, however, propose to enter further into previous work on this subject here, for it will be necessary frequently to refer to the chief authorities in the course of this revision of the genus.

In attempting here to reclassify the British *Lepidostrobi* occurring as incrustations in the Coal Measures, I take as my specific unit the shape of the sporophyll.

I am unable to find any critical characters, whether derived from the features of the axis of the cone, or from any other details of its organisation, which are at all comparable in taxonomic value to the sporophyll-form.

The sporophylls of these cones have naturally two regions, the proximal and the distal. The proximal portion, often called the pedicel, is the lower part of the sporophyll, including the attachment to the axis and the surface bearing the sporangium. The position of the ligule marks the distal extremity of this region, and this rudimentary organ, of course, indicates that morphologically this portion of the sporophyll is an expanded leaf base. Very often part of the pedicel, especially that subtending the sporangium, is modified by the formation of a cushion or other enlarged growth, on which the sporangium is seated or to which it is attached. The distal portion of the sporophyll, often termed the lamina, extending from the region of the ligule to the apex of the sporophyll, is as a rule less modified, *i. e.*, more leaf-like, than the pedicel. Yet modifications sometimes occur here also, as, for instance, the development of a downwardly directed heel in the region of the ligule.

In most impressions of *Lepidostrobi*, it is usually possible to make out the essential features of both regions of the sporophyll, and it is on these characters that the species should be founded. Whether the cone is homosporous or heterosporous does not affect the question, for, as we know, the sporophylls subtending the micro- and megasporangia of the same cone are alike, and often precisely similar to those of homosporous cones.

From the study of considerable material, consisting of various cones of the *Lepidostrobus* type, preserved in the Sedgwick Museum, Cambridge,

many of which have been collected by myself, I have come to the conclusion that the cones fall into three groups or subgenera, which may be conveniently described as follows:—

Eulepidostrobus. Cones in which the sporophylls are comparatively leaf-like, with no great dissimilarity in size or shape between the pedicel and the lamina, e. g. *L. variabilis*, Lindl. & Hutt.

Ortholepidostrobus. Cones in which the distal portion of the sporophylls or laminæ are greatly expanded and developed as compared with the proximal regions or pedicels, e. g. *L. majus*, Brongn.

Sublepidostrobus. Cones in which the proximal portions of the sporophylls are much better developed than the distal regions or laminæ, e. g. *L. Jacksoni*, Arb.

The *Eulepidostrobi* are the most difficult group from a taxonomic standpoint. I am inclined to recognise only one species in Britain, *L. variabilis*, Lindl. & Hutt., where other authors distinguish several. There are, it is true, enormous differences in both size and shape between cones of this species and the strobili known as *L. Geinitzi*, Schimp., and *L. ornatus*, Brongn., but I can find no real macroscopic differences in the form of the sporophylls which can be clearly made out in impressions. No doubt such differences do exist, and, had we to deal with nothing but petrifications of these cones, we might discriminate further species founded on small characters. But the fact remains that these cones are so stereotyped that viewed merely as impressions it is not possible to discriminate between them except in respect of size, always a dangerous index in taxonomy. It is thus better to recognise the limitations of our powers in this direction by referring these fossils to one stereotyped species, than to attempt to specify a number of types which cannot be clearly distinguished from one another. The case of *L. variabilis* is exactly "on all fours" with that of *Stigmaria ficoides*.

The *Ortholepidostrobi** have at least one feature in which they stand apart from other members of the genus, i. e. the caducous nature of the sporophylls. In the other two groups the sporophylls are remarkably persistent, and it is rare to find among them a *Lepidostrobus* axis which is not fully clothed with sporophylls. In the case of the *Ortholepidostrobi*, the sporophylls are so easily detached from the axis that until a few years ago they were only known in the isolated state. They were then generally referred to the genus *Lepidophyllum*, e. g. *Lepidophyllum lanceolatum*, Lindl. & Hutt. The present paper contains the first figured examples of more than one type of these sporophylls still attached to the axis of the cone. In regard to all the British types here described, it may be now regarded as proved that they are not foliar leaves, as was at one time thought, but the sporophylls of a cone, and thus they are best referred to the genus *Lepidostrobus*. The genus

* The term "ortho" in the sense of "erect" recalls the very erect position of the laminas of the sporophylls of these cones.

Lepidophyllum should be restricted to Lycopod leaves, pure and simple. If, in making a record of one of these cones, only a detached sporophyll is known from a particular locality, the fact can be illustrated as in the following example :—*Lepidostrobis lanceolatus*, Lindl. & Hutt. [Sporophyll].

The *Sublepidostrobi* are the rarest and least known type in Britain, and in no case have we any complete knowledge of the sporophylls except the distal portions.

SYNOPSIS OF SPECIES.

1. Subgenus EULEPIDOSTROBUS, n. n.

Lepidostrobis variabilis, Lindl. & Hutt.

L. Russellianus, Binney.

2. Subgenus ORTHOLEPIDOSTROBUS, n. n.

L. brevifolius (Lesq.).

L. hastatus (Lesq.).

L. intermedius (Lindl. & Hutt.).

L. lanceolatus (Lindl. & Hutt.).

L. longibracteatus (Prestw.).

L. majus (Brongn.).

L. minor (Goode).

L. Moyseyi, sp. nova.

L. radians, Schimper.

L. triangularis (Zeiller).

3. Subgenus SUBLEPIDOSTROBUS, n. n.

L. Jacksoni, Arber.

L. ? spinosus, Kidst.

Subgenus EULEPIDOSTROBUS, n. n.

LEPIDOSTROBUS VARIABILIS, Lindl. & Hutt. (Pl. 8. figs. 1, 2, 3.)

1828. *Lepidostrobis ornatus*, Brongniart, Prod. Hist. Végét. Foss. p. 47.

*1831. *Lepidostrobis variabilis*, Lindl. & Hutt., Foss. Flora, vol. i. pl. 10, pl. 11 (right-hand fig.).

1831. *Lepidostrobis ornatus*, Lindl. & Hutt., *ibid.* vol. i. pl. 26 (1831).

1837. *Lepidostrobis ornatus* var. *didymus*, Lindl. & Hutt., *ibid.* vol. iii. pl. 163.

*1838. *Lepidostrobis* sp., Brongniart, Hist. Végét. Foss. vol. ii. pl. 23. figs. 1a to e, 2a to e, pl. 25. figs. 3 & 4 a to c.

*1838. *Lepidostrobis* sp., Brongniart, *ibid.* vol. ii. p. 49. pl. 22. figs. 5-7.

1847. *Lepidostrobis ornatus*, Hook. f., in Mem. Geol. Surv. vol. ii. pt. 2, p. 448, pl. 7, pl. 8. figs. 1-11.

1850-56. *Lepidostrobis ornatus*, Bronn, Leth. Geogn. vol. i. pt. 2, p. 127, pl. 6. figs. 6-12.

1855. *Lepidostrobis variabilis*, Geinitz, Vers. Steinkohlenf. Sachs. p. 50, pl. 2. figs. 1, 3, 4.

* Indicates figures of typical examples.

1855. *Lepidostrobus ornatus*, Goldenburg, Flora Sarapontana Foss. Heft i, p. 34, pl. B. figs. 3-5.
1869. *Lepidostrobus variabilis*, Roehl, Paläontogr. vol. xviii. p. 142, pl. 7. fig. 2.
1870. *Lepidostrobus Geinitzii*, Schimp., Traité Pal. Végét. vol. ii. p. 62, pl. 61. fig. 6.
- *1870. *Lepidostrobus variabilis*, Schimp., *ibid.* vol. ii. p. 61, pl. 58. figs. 2 a & 5; pl. 61. figs. 1, 2; pl. 62. figs. 35, 35 b.
1875. *Lepidostrobus variabilis*, Feistmantel, Paläontogr. vol. xliii. p. 218, pl. 43. pl. 44. figs. 1-2.
- *1886-88. *Lepidostrobus variabilis*, Zeiller, Flore Foss. Bass. Houill. Valenciennes, p. 499, pl. 76. figs. 3-4.
- 1886-88. *Lepidostrobus ornatus*, Zeiller, *ibid.* p. 497, pl. 76. figs. 5-6.
- 1886-88. *Lepidostrobus Geinitzi*, Zeiller, *ibid.* p. 501, pl. 76. fig. 2.
1890. *Lepidostrobus Geinitzi*, Renault, Étud. Terr. Houill. Commentry. Flore Foss. pt. 2, p. 527, pl. 61. figs. 5, 6.
1893. *Lepidostrobus squarrosus*, Kidston, in Trans. Roy. Soc. Edinb. vol. xxxvii. pt. 2, p. 342, pl. 4. figs. 13, 13 a, & 14.
- *1900. *Lepidostrobus* sp., Arber, Fossil Plants, p. 68, fig. 13.

Diagnosis.—Cones cylindrical, elongated, not very narrow, very variable in size and shape, from 7×1 cm. to 15×4 cm. or more. Lamina (distal portion of sporophyll) lanceolate, small, erect, short. Cones homosporous.

States of preservation.—These cones occur in the shales and clay-ironstone nodules of the Coal Measures in various states of preservation. Some examples show the true external surface, *i. e.* all that is seen is the imbricated series of sporophyll laminae. Very often, however, the greater number of the laminae, or distal portions of the sporophylls, are broken off or have undergone considerable decay before preservation. This is of particular frequency in the case of specimens occurring in clay-ironstone, and such examples may bear a very different appearance to the perfect cone. Such specimens have been frequently described as a distinct species, *L. ornatus*. The specimens described by Hooker in 1847 are good examples. Other impressions represent longitudinal sections through the cone, which may be either radial (in which event the axis is seen) or tangential. It is only in the former case that the characters of the sporophylls can be ascertained.

Remarks.—*L. variabilis* as here defined is an extremely variable species. All gradations may be found between small and large cones with very slight differences in the shape of the sporophylls, depending chiefly on the size of the cone. A large type of cone has been distinguished by several authors under the name *L. Geinitzi*, Schimp., but of the figures accompanying these descriptions those of Schimper, Zeiller, and Renault (see above synonymy) alone show the characters of the sporophylls clearly. This type of cone is admittedly much longer and stouter than the ordinary forms of *L. variabilis*, but I am unable to see any real distinction worthy of specific rank as regards the characters of the sporophylls. Schimper in founding the species simply figures two sporophylls, which, except in size, appear to

* Indicates figures of typical examples.

me to be identical with those of *L. variabilis*. The differences between the two species indicated by Zeiller appear to me to be very slight, in some cases non-existent—a view which Renault's figures confirm. I therefore conclude that, unless an appeal is to be made to mere size and shape, which are notoriously untrustworthy taxonomic guides, there is no real distinction between the sporophylls of *L. Geinitzi* and *L. variabilis*. The two cones may be really distinct, but when they are preserved as impressions, there are no distinctly visible characters by which they may be distinguished.

In the case of *L. squarrosus*, again, according to Kidston the chief differences between that species and *L. variabilis* are the former's "larger size, and the much more lax spreading nature of the bracts." These characters do not appeal to me as worthy of specific rank.

Two very interesting and exceptional impressions of isolated sporophylls of this species are figured on Pl. 8. figs. 1, 2, & 3. Both are from the Middle Coal Measures of the Kent Coalfield.

No. 2242*. Fig. 1, Pl. 8, shows one example, natural size, and the same organ is shown enlarged twice in fig. 2. The lamina of the sporophyll is seen on the right, and on the left the sporangium. The ligule can be clearly seen between the two organs. The structure seen on the left is another sporophyll, and not the axis. The sporangium measures 10 mm. radially and is about 6 mm. high.

No. 3201. In another example shown on Pl. 8. fig. 3 (natural size), the sporophyll is still attached to the axis. The sporangium here measures 7.5 mm. across and 4.5 mm. high.

Cones of the *Lepidostrobus variabilis* type are known to have been borne by several stem-species of *Lepidodendron*, viz.:—

Lepidodendron lycopodioides, Sternb. (including *L. lunceolatum*, Lesq.).

L. ophiurus, Brongn.

? *L. loricatum*, Arber.

Types. Lindley and Hutton's in the Hancock Museum, Newcastle-on-Tyne.

Distribution. Known from all horizons in the Coal Measures and from nearly all coalfields.

LEPIDOSTROBUS RUSSELLIANUS, Binney.

1871. *Lepidostrobus Russellianus*, Binney, in Pal. Soc. (Observ. Struct. Foss. Plants, Part II.), p. 51, pl. 9. figs. 1, 1 a, 2, & 2 a.

1871. *Lepidostrobus* (?) *dubius*, Binney, *ibid.*, p. 52, pl. 9. figs. 3 & 3 a.

1871. *Lepidostrobus tenuis*, Binney, *ibid.*, p. 53. pl. 9. figs. 4 & 4 a.

1871. *Lepidostrobus levidensis*, Binney, *ibid.*, p. 54, pl. 10. figs. 1, 1 a, & 1 b.

1912. ? *Lepidostrobus* cf. *Russellianus*, Vernon, in Quart. Journ. Geol. Soc. vol. lxxviii. p. 621, pl. 59. fig. 1.

* The numbers refer to the Carboniferous Plant Collections, Sedgwick Museum, Cambridge.

Diagnosis.—Cones similar to those of *L. variabilis*, Lindl. & Hutt., but heterosporous.

Remarks.—It may be questioned whether heterospory is a sufficiently important character to act as a specific index by itself. I am, however, inclined to maintain Binney's species chiefly on the grounds of convenience.

Type. No. 471. Carbon. Plant Coll., Sedgwick Museum, Cambridge. Also 472 (*Lepidostrobus* ? *dubius*, Binney).

Distribution. Lower and ? Middle Coal Measures.

Lower Coal Measures :—Blackband Ironstone near Airdrie, Lanarkshire.

Middle Coal Measures :—Thick Coal, Chilvers Coton, Warwickshire.

Subgenus ORTHOLEPIDOSTROBUS, n. n.

LEPIDOSTROBUS BREVIFOLIUS (Lesq.). (Pl. 8. figs. 4, 5, 6, 7, 8.)

Sporophylls detached.

1858. *Lepidophyllum brevifolium*, Lesq., in Rogers, Geol. Pennsylv. vol. ii. pt. 2, p. 876, pl. 17. fig. 6.

1879-80. *Lepidophyllum brevifolium*, Lesq., Coal Flora Pennsylv. p. 417, pl. 69. fig. 33.

1888. *Lepidophyllum* sp., Kidston, in Trans. Roy. Soc. Edinb. vol. xxxiii. pt. 2, p. 395, pl. 27. figs. 7 a, 7 b.

1912. *Lepidophyllum brevifolium*, Arber, Phil. Trans. Roy. Soc. ser. B. vol. ccii. p. 252.

Diagnosis.—Sporophylls small, up to 1·8 cm. in length and 7-12 mm. across at the greatest width. Pedicel extremely narrow, keeled, very elongately wedge-shaped, about 8-10 mm. long. Lamina shortly triangular, often nearly equilateral, lower angles somewhat incurved towards the pedicel, about 7 to 12 mm. broad at the base, which is usually the broadest part.

Remarks.—The sporophylls of this species are, with exception of the specimen figured here, not yet known attached to the cone axis.

No. 1249. The specimen figured on Pl. 8. fig. 4, natural size, and enlarged twice on Pl. 8. fig. 5, is a medium-sized example of a detached sporophyll. The whole length of the pedicel is probably not disclosed. The region has a distinct keel.

No. 1250. Another not very perfect specimen is shown on Pl. 8. fig. 7, natural size. The pedicel here has a broad expansion on either side of the keel, and this may possibly be a flattened sporangium.

No. 1257. One of the largest examples known to me is shown natural size on Pl. 8. fig. 8. This sporophyll exceeds 17 mm. in length and 10 mm. in breadth. What appear to be traces of a sporangium are seen around the keel of the pedicel.

No. 1266. On Pl. 8. fig. 6 a specimen is shown natural size in which several sporophylls appear to be attached to an axis. The impression, however, is not very clear, and the laminas are alone distinctly seen.

Distribution. Horizon: Upper Coal Measures.

Coalfields:—Somerset—Bristol; Radstock Series at Radstock, Timsbury, etc. Forest of Dean, Park Gutter Colliery (Yorkley Coal).

LEPIDOSTROBUS HASTATUS, Lesq. (Pl. 8. figs. 9 & 10.)

Sporophylls attached and detached.

1858. *Lepidophyllum hastatum*, Lesq., in Rogers, Geol. Pennsylv. vol. ii. pt. 2, p. 876, pl. 17. fig. 7.

1866. *Lepidostrobus hastifolius*, Lesq., Geol. Surv. Illinois, vol. ii. Palæontol. p. 456.

1879-80. *Lepidostrobus hastatus*, Lesq., Coal Flora Pennsylv. p. 438, pl. 69. figs. 27 & 28.

Diagnosis.—Cone small, ovate. Sporophylls small, hastate, up to 2.5 cm. long and 7 mm. across at their greatest width. Pedicel wedge-shaped, narrow, about 1 cm. in length. Lamina about 1-1.5 cm. long and 5-7 mm. across at the base, all angles, especially the lateral, acute.

Remarks.—The present is the first British record of the species, and the only specimens so far known are detached sporophylls. Lesquereux has, however, figured a cone of this species. An excellent specimen from the Transition Coal Measures of Kent is seen on Pl. 8. fig. 9, natural size. Another example from the Upper Coal Measures of the Somerset Coalfield is seen slightly enlarged on Pl. 8. fig. 10.

Distribution. Upper and Transition Coal Measures.

Upper Coal Measures.

Coalfield:—Somerset—Bristol, Coal Pit Heath, Bristol.

Transition Coal Measures.

Coalfield:—Kent, Bishopbourne Boring.

LEPIDOSTROBUS INTERMEDIUS (Lindl. & Hutt.). (Pl. 8. figs. 11, 12, 13.)

Sporophylls detached.

1831. *Lepidophyllum intermedium*, Lindl. & Hutt., Foss. Flora, vol. i. pl. 43 fig. 3.

1877. *Lepidophyllum lanceolatum*, Lebour., Illustr. Fossil Plants, p. 105, pl. 53.

1870-72. *Lepidophyllum intermedium*, Schimp., Traité Pal. Végét. vol. ii. p. 72.

1890. *Lepidophyllum majus*, Renault, Flore Foss. Terr. Houill. Commentry, pt. 2, p. 516, pl. 59. figs. 8-9.

1904. *Lepidophyllum majus*, Zalessky, in Mém. Com. Géol. St. Pétersbourg, N. S. Livr. 13, p. 104, pl. 7. fig. 6.

Sporophylls attached.

1916. *Lepidostrobus intermedius*, Arber, in Phil. Trans. Roy. Soc. ser. B, vol. ccviii. p. 146, pl. 4, fig. 21.

Diagnosis.—Cone large, short, cylindrical, about 2-3 cm. in diameter. Sporophylls large, 3-9 cm. in length, narrowly lanceolate, uninerved, faintly striated; striæ radiating, and not extending to apex. Apex acuminate.

Remarks.—The sporophylls of this species, hitherto only known in the detached state, were recently figured by the author from South Staffordshire,

still in continuity with the axis. In the specimen in question the sporophylls were rather small (only 3–4 cm. long), whereas they are usually about 6 cm. in length and may even attain to 9 cm. Several cones with larger sporophylls still attached are figured here from Dr. Moysey's collection from the Middle Coal Measures of Derbyshire. In each case the laminae of the sporophylls are narrowly lanceolate, not more than 3 mm. broad, and the apex is markedly acuminate. These seem to be the chief characters of the species.

No. 4014. On Pl. 8. fig. 11 a cone is seen, natural size, showing the external surfaces of markedly acuminate sporophylls. Below the cone is broken across radially and shows two sporangia on each side of the axis. The length of the lamina of the sporophyll is 7·3 cm. and that of the pedicel exceeds 7 mm.

No. 4015. Another cone, also fractured obliquely below, is figured natural size on Pl. 8. fig. 12. Here the lamina exceeds 4 cm. in length and the pedicel is at least 8 mm. long.

No. 4016. A further cone with sporophylls attached is seen on Pl. 8. fig. 13. The sporophylls are here very clearly seen. They are between 4–5 cm. in length and the greatest breadth is about 5 mm.

Type. Lindley and Hutton's in the Hancock Museum, Newcastle-on-Tyne.

Distribution. Lower to Transition Coal Measures.

Transition Coal Measures.

Coalfields:—Le Botwood. Shrewsbury. Warwickshire.

Middle Coal Measures.

Coalfields:—Kent. South Staffordshire. ? Notts and Derby.

Lower Coal Measures.

Coalfields: Notts and Derby. Lanarkshire.

LEPIDOSTROBUS LANCEOLATUS (Lindl. & Hutt.). (Pl. 8. figs. 14, 15, 16, 17.)

Sporophylls detached.

1831. *Lepidophyllum lanceolatum*, Lindl. & Hutt. vol. i. pl. 7. figs. 3 4.

1855. *Lepidophyllum lanceolatum*, Geinitz, Vers. Steinkohlenf. Sachsen, p. 50, pl. 2. fig. 8.

1858. *Lepidophyllum lanceolatum*, Lesq., in Rogers, Geol. of Pennsylv. vol. ii. pt. 2, p. 875, pl. 17. fig. 1.

1868. *Lepidophyllum lanceolatum*, Roehl, Foss. Flora Steink. Form. Westphal. in Palæontogr. xviii. p. 141, pl. 28. fig. 10.

1879–80. *Lepidostrobus lanceolatus*, Lesq., Coal Flora Pennsylv. p. 436, pl. 59. fig. 38.

1886–88. *Lepidophyllum lanceolatum*, Zeiller, Flore Foss. Bass. Houill. Valenciennes, p. 505, pl. 77. fig. 7.

1899. *Lepidophyllum lanceolatum*, Zeiller, Étude Flore Foss. Bass. Houill. Mécracée, p. 75, fig. 11 on p. 50.

1900. *Lepidophyllum lanceolatum*, Zeiller, Élémt. Palæobot. p. 187, fig. 129.

1904. *Lepidophyllum lanceolatum*, Zalessky, in Mém. Com. Géol. St. Pétersb., N.S. Livr. 13, p. 104, pl. 6. fig. 2; pl. 7. fig. 10.
 1907. *Lepidophyllum lanceolatum*, Zalessky, in Bull. Com. Géol. St. Pétersb. vol. xxvi. No. 134, p. 384, pl. 13. fig. 12.
 1907. *Lepidophyllum lanceolatum*, Zalessky, *ibid.* vol. xxvi. p. 498, pl. 18. fig. 7.
 1911. *Lepidophyllum lanceolatum*, Kidston, in Mém. Mus. Roy. Hist. Nat. Belgique, vol. iv. p. 153.

Sporophylls attached.

1855. ? *Sagenaria dichotoma* (= *Lepidostrobus lepidophyllaceus*), (Leinitz, Vers. Steinkohlenf. Sachs. p. 34, pl. 2. fig. 7.
 1870. *Lepidostrobus oblongifolius*, Lesq., Geol. Rep. Illinois, vol. iv. p. 441, pl. 30. figs. 3, 3 b.
 1879-80. *Lepidostrobus oblongifolius*, Lesq., Coal Flora Pennsylv. vol. ii. p. 437, pl. 69. fig. 29.
 1886-88. *Lepidophyllum lanceolatum*, Zeiller, Flore Foss. Bass. Houill. Valenciennes, p. 505, pl. 77. fig. 8.
 1899. *Lepidostrobus variabilis*, Hofmann & Ryba, Leitpflanzen, p. 86, pl. 16. fig. 6.

Diagnosis.—Sporophyll lanceolate, or slightly ovate-lanceolate, between 4 and 5 cm. long and 5-10 mm. (usually 7 or 8 mm.) broad at its widest part. Lamina acute and sometimes distinctly acuminate. Pedicel about 1 cm. long, wedge-shaped, lower angle acute. Nerve often broad, prominent.

Remarks.

V. 2944. A specimen from the British Museum (Nat. Hist.), from the Upper Coal Measures of Somerset, is figured natural size on Pl. 8. fig. 14. It shows the laminas of several sporophylls of the broader type very clearly.

No. 2415. A small sporophyll from the Transition Coal Measures of Kent is figured natural size on Pl. 8. fig. 15. The tip of the apex is not seen. This sporophyll exceeds 4 cm. in length, but is only 6 mm. across at its greatest width.

No. 2904. Another large sporophyll from the Middle Coal Measures of Pembrokeshire is seen natural size on Pl. 8. fig. 16. It exceeds 4.8 cm. in length, the tip not being disclosed, and is 7 mm. across at its widest part.

No. 2417. The base of a sporophyll from the Transition Coal Measures of Kent is shown enlarged on Pl. 8. fig. 17 to illustrate the pedicel in this species.

Type. Lindley and Hutton's in Hancock Museum, Newcastle-on-Tyne.

Distribution. Lower to Upper Coal Measures.

Upper Coal Measures.

Coalfields:—Radstock. South Staffordshire.

Transition Coal Measures.

Coalfields:—Kent. Wyre Forest South. North Staffordshire. South Lancashire.

Middle Coal Measures.

Coalfields:—Kent. South Welsh. Pembrokeshire. Wyre Forest North (Lower). North Staffordshire. Notts and Derby. Yorkshire. South Lancashire. Fife.

Lower Coal Measures.

Coalfields:—North Staffordshire. South Lancashire. Newcastle-Durham. Ayrshire. Lanarkshire.

LEPIDOSTROBUS LONGIBRACTEATUS (Prestw.) *. (Pl. 8. figs. 18 A & B, and 19 A & B.)

1840. *Lycopodites ? longibracteatus*, Prestwich, in Trans. Geol. Soc. ser. 2, vol. v. p. 488, pl. 38. figs. 9-11.

Diagnosis.—Axis 3-5 mm. in diameter. Lamina of sporophyll about 5 cm. long by 8 mm. in width at widest part; apex acute; fairly prominent midrib; closely parallel lateral veins meeting the midrib at an acute angle. Pedicel of sporophyll broadest at junction with lamina; greatest width apparently about 6 mm. and length 6-8 mm. Sporangium about 4-6.5 mm. long by 2-4.5 mm. high.

Remarks.—This is the cone of *Lepidophloios acerosus* (Lindl. & Hutt.), found by Prestwich in continuity with that stem. So far as I am aware, this species has not been described since. It is nearly allied to *Lepidostrobus intermedius* (Lindl. & Hutt.) and *L. lanceolatus* (Lindl. & Hutt.), but I think it is probably distinct from both these species. Williamson (Organisation, etc., pt. 19, 1893, pl. 8. fig. 54) refigures Prestwich's type by means of a very inadequate drawing, and also figures another specimen, from Aber Sychan (Brit. Mus. V. 4261), which he regards as belonging to the same species. It is certainly closely similar, but, if specifically identical, it represents a more massive example than the type-specimen.

Type. British Museum (Nat. Hist.), type. The type-specimens are refigured on Plate 8. figs. 18 A & B and 19 A & B. Figure 18 A shows the cone at the end of a branch (nat. size), while the cone is represented on a larger scale in fig. 18 B. Fig. 19 A shows the specimen from which Prestwich's pl. 38. fig. 9 was drawn; fig. 19 B is a photograph of the other half of the same nodule.

Distribution. Middle Coal Measures.

Coalfield:—Coalbrookdale.

* [I am mainly responsible for this section. I am indebted to Mr. W. N. Edwards of the British Museum (Nat. Hist.) for much kind help both in connection with the literature and in tracing the type-specimens.—A. A.]

LEPIDOSTROBUS MAJOR (Brongn.). (Pl. 8. fig. 20 and Pl. 9. fig. 21.)

Sporophylls detached.

1822. *Filicites (Glossopteris) dubius*, Brongn. Sur Class. Végét. Foss. p. 232 (footnote), pl. 13 (=2), fig. 4.
1828. *Lepidophyllum majus*, Brongn. Prodr. Hist. Végét. Foss. p. 87.
1835. *Lepidophyllum trinerve*, Lindl. & Hutt. Foss. Flora, vol. ii. pl. 152.
1836. *Lepidophyllum glossopteroides*, Goepf., Syst. Filic. Foss. in Nov. Act. Acad. Cies. Leop.-Car. vol. xvii. Supp. p. 431, pl. 44. fig. 3.
1854. *Lepidophyllum majus*, Geinitz, Flora Hainschen-Ebersdorf. p. 55, pl. 14. figs. 12-14.
1855. *Lepidophyllum majus*, Geinitz, Verstein. Steinkohleuform. Sachsen, p. 37, pl. 2. fig. 5.
1862. *Fruchtblatt von Lepidophloios larinus*, Goldenberg, Flora Saraepou. Foss. Heft 3, pp. 34 & 45, pl. 15. fig. 5.
1870. *Lepidophyllum majus*, Schimp., Traité Pal. Végét. vol. ii. p. 72, pl. 61. fig. 8†; pl. 64. fig. 9.
1871. *Lepidophyllum majus*, Feistmantel, Abhandl. K. Böhm. Gesell. Wissen. VI. Folge, Band v. p. 31, pl. 1. figs. 2-3.
- 1845-75. *Lepidophyllum majus*, Feistmantel, Palæontogr. vol. xxiii. p. 41, pl. 42. figs. 2-4 († fig. 1).
1877. ? *Lepidophyllum binerve*, Lebour, Illustr. of Fossil Plants, p. 103, pl. 52.
1901. *Lepidophyllum* († *Lepidostrobus*) *majus*, Kidston, in Trans. Nat. Hist. Soc. Glasgow, N. S. vol. vi. pt. 1, p. 63, fig. 9.
1911. *Lepidophyllum majus*, Kidston, in Mém. Mus. Roy. Hist. Nat. Belgique, vol. iv. p. 154.
1912. *Lepidophyllum majus*, Arber, in Phil. Trans. Roy. Soc. ser. B, vol. ccii. p. 251.

Diagnosis.—Sporophylls very large, up to 12 cm. long, rarely less than 10 cm. in length, and almost 1.5 cm. broad, lanceolate, acuminate, with a prominent median nerve in the lower part and a very marked groove above. Pedicel wedge-shaped, about 2 cm. long and 1 cm. across at its widest part.

Remarks.—No examples of these sporophylls attached to an axis are known from Britain. Dr. David White, however, in his "Fossil Flora of the Lower Coal Measures of Missouri" (Monogr. 37, U.S. Geol. Survey, 1899), has figured (pl. 60) a cone *Lepidostrobus missouriensis*, D. White, with very similar sporophylls apparently attached to an axis. The sporophylls are more oval-lanceolate (2 cm. broad) than in *L. majus*. While the two species may be distinct, the American specimen appears to leave little doubt that the organs known as *L. majus* were sporophylls and not leaves.

No. 2076. An almost perfect sporophyll of this species from the Bristol Coalfield is figured on Pl. 8. fig. 20, nat. size. It measures 11 cm. in length, and 1.4 cm. across at its widest part. In the centre of the lamina there are two parallel and rather broad ridges rather distant from one another and separated by a shallow groove. The basal angles of the lamina are slightly eared.

No. 3830. On Pl. 9. fig. 21 part of the pedicel of a sporophyll of this species is shown, enlarged three times to exhibit the reticular network which

is sometimes seen in this region, and which may represent the carbonised sporangial wall.

Distribution. Lower to Upper Coal Measures.

Upper Coal Measures.

Coalfields:—Radstock—Bristol. Forest of Dean.

Middle Coal Measures.

Coalfields:—Notts and Derby. Yorkshire. South Lancashire.

Lower Coal Measures.

Coalfields:—South Lancashire.

LEPIDOSTROBUS MINOR (Goode). (Pl. 9. figs. 22, 23, 24, 25.)

Sporophylls detached.

1913. *Lepidophyllum minus*, Goode, in Quart. Journ. Geol. Soc. vol. lxi. p. 266, pl. 28. figs. 3 & 5.

1914. *Lepidophyllum minus*, Arber, in Quart. Journ. Geol. Soc. vol. lxx. p. 78.

1914. *Lepidophyllum brevifolium*, Arber, in Phil. Trans. Roy. Soc. ser. B, vol. cciv. p. 386.

Diagnosis.—Sporophyll small, sagittate, up to 15 mm. long and 5–7 mm. wide at the broadest part. Pedicel slender, elongately wedge-shaped, 5–7 mm. long and 2–3 mm. wide at the broadest part. Lamina short, triangular, nearly equilateral, about 1 cm. long, lower angles somewhat recurved towards the pedicel.

Remarks—This species stands near to *L. brevifolius*, but the pedicel is larger, the lateral margins straighter, and the angles are more acute. The basal angles of the pedicel are more prolonged and curved downwards.

The specimens from the Wyre Forest which in 1914 I attributed to *Lepidophyllum brevifolium* should be included under this species.

Nos. 2902, 2903. One of the type-specimens from Pembrokeshire is refigured (natural size) on Pl. 9. figs. 22 & 23.

Other specimens from the Kent coalfield are figured on Pl. 9. figs. 24 and 25, both natural size.

No. 2448. Fig. 24 is a small example, only 12 mm. long.

No. 2295. Fig. 25 shows a larger specimen 18 mm. long, and a very broad example 9 mm. across.

Type. No. 2902–3. Carbon. Plant Coll., Sedgwick Museum, Cambridge.

Distribution. Middle Coal Measures.

Coalfields:—Kent. Pembrokeshire. Wyre Forest North (Lower).

LEPIDOSTROBUS MOYSEYI, sp. nova. (Pl. 9. figs. 26 & 27.)

Diagnosis.—Sporophyll small, 3 cm. long and 8 mm. broad, shovel-shaped, apparently concave; lamina 2.2 cm. long, triangular; base nearly straight;

pedicel very narrowly and elongately wedge-shaped, 8 mm. long. Apex bluntly acute.

Remarks.—This rare type in Dr. Moysey's collection is figured on Pl. 9. fig. 26, natural size, and nearly twice enlarged in fig. 27. In the shape of the lamina it appears to me to differ from any other sporophyll known to me, though it may approach to Lesquereux's *L. ovatifolius* ('Coal Flora,' vol. ii. p. 438, pl. 69. fig. 32).

Type. No. 4018. Carbon. Plant Coll., Sedgwick Museum, Cambridge.

Distribution. Middle Coal Measures.

Coalfields :—Notts and Derby.

LEPIDOSTROBUS RADIAN, Schimper. (Pl. 9. figs. 28, 29, 30, 31.)

Sporophylls attached.

1838. *Lepidostrobis* sp., Brongn., Hist. Végét. Foss. vol. ii. pl. 23. fig. 6.

[— *Conophoroides anthemis*, König, Icones Foss. Sectil.† pl. 13. fig. 200.]

1870. *Lepidostrobis radians*, Schimp., Traité Pal. Végét. vol. ii. p. 63.

1899. † *Lepidophyllum Jenneyi*, White, Monogr. 37, U.S. Geol. Surv. p. 214, † pl. 59. fig. 1 a.

1901. *Lepidostrobis anthemis*, Kidston, in Trans. Nat. Hist. Soc. Glasgow, N. S. vol. vi. p. 62, fig. 8.

Sporophylls detached.

*1899. *Lepidophyllum Jenneyi*, White, Monogr. 37, U.S. Geol. Surv. p. 214, pl. 59. fig. 1 b, fig. 2; † pl. 63. fig. 6.

Diagnosis.—Dimensions and shape of cone unknown. Sporophylls small or of medium size, broadly elliptical, length 1·5–2 cm., usually about 2 cm., greatest breadth 7–10 mm., usually about 8 cm. Pedicel similar in shape to the lamina, but usually distinctly shorter.

Remarks.—This cone is distinctly rare in Britain. No specimen of the complete cone, seen in surface-view, is known. A very few examples of what is practically a transverse section of the cone have been found, with the sporophylls all spread out in one plane, and also of detached sporophylls.

This cone has hitherto been known as *Lepidostrobis anthemis*, König. König's memoir, entitled "Icones Fossilium Sectiles," was, however, never published, though copies were widely distributed about the year 1851 on the death of the author. The lack of formal publication appears to me to render invalid the new generic and specific names contained in this memoir, and it is therefore necessary to fall back on Schimper's *Lepidostrobis radians*, expressly proposed for the specimen originally figured without specific determination by Brongniart.

No. 67. On Pl. 9. fig. 28 several sporophylls are seen, natural size, still attached to an axis.

* Indicates figures of typical examples.

† This memoir was never published, see Bibliography, 19.

No. 78. A single sporophyll 2 cm. long is shown, natural size, on Pl. 9. fig. 29. The pedicel here appears to be only a little smaller than the lamina.

No. 81. A still larger specimen, also figured natural size on Pl. 9. fig. 30, is 2·3 cm. long, and the lamina is distinctly larger than the pedicel.

No. 65. A smaller and narrower specimen is shown on Pl. 9. fig. 31, natural size.

Distribution. Middle to Transition Coal Measures.

Transition Coal Measures.

Coalfields :—North Staffordshire. South Lancashire.

Middle Coal Measures.

Coalfields :—Pembrokeshire. Yorkshire. South Lancashire.

LEPIDOSTROBUS TRIANGULARIS (Zeiller). (Pl. 9. figs. 32 & 33.)

Sporophylls detached.

1886-88. *Lepidophyllum triangulare*, Zeiller, Flore Foss. Bass. Houill. Valenciennes, p. 508, pl. 77. figs. 4 & 5.

1897. *Lepidophyllum Pichleri*, Kerner, in Jahrb. k.k. Geol. Reichsanst. vol. xlvii. Heft 2, p. 383, pl. 10. figs. 1-2.

Sporophylls attached.

1910. *Lepidostrobis triangularis*, Arber, in Proc. Yorks. Geol. Soc. vol. xvii. pt. 2, p. 149, pl. 16. fig. 3.

Diagnosis.—Cone cylindrical, rather small, 7 or more cm. long and about 2 cm. across. Sporophyll markedly hastate. Pedicel wedge-shaped, smaller than the lamina, 5-8 mm. long, 3-5 mm. broad at its widest point, with a single nerve. Lamina triangular, the sides somewhat concave, lower angles prolonged, acute, somewhat turned inwards towards the pedicel, 12-15 mm. long, 8-12 mm. broad at the base, sharply pointed at summit, with a single median nerve.

Remarks.—This is an infrequent type in Britain, and the sporophylls usually occur detached. The only known specimen of a nearly complete cone of this species is one collected by Dr. Moysey, which I figured some years ago from the Middle Coal Measures of Derbyshire, and which is figured here natural size on Pl. 9. figs. 32 A & B. The cone was a small one, about 7 cm. in length and 2 cm. across at its widest point. The late Professor Zeiller, who saw this specimen, agreed that it was identical with his *Lepidophyllum triangulare*. Part of the stalk of the cone is seen at the base of this specimen, but this organ is incompletely preserved, and it is thus impossible to say whether this cone should be attributed to a *Lepidodendron* or a *Sigillaria*. In some respects the sporophylls recall those of certain species of *Sigillariostrobus*.

Dr. Kidston (18. p. 136) has recently concluded that *L. triangularis* is closely related to the species here termed *L. radians*, Schimper, and, "if really distinct from it, differs only in the sides of the bracts being perhaps somewhat more concave." To my mind, however, these two species are quite distinct in the shape of the sporophyll as a whole, and especially in the dissimilarity in the size and shape of the lamina and pedicel, and in the prolongation of the lateral angles of the former, as a comparison of figs. 28-31 with figs. 32 and 33 will show.

On Pl. 9. fig. 33 a detached sporophyll is shown.

Type. ? Museum of École des Mines, Paris.

Distribution. Middle Coal Measures.

Coalfields:—South Welsh. South Staffordshire. North Staffordshire.
Notts & Derby. Yorkshire.

Section *Sublepidostrobus*.

LEPIDOSTROBUS JACKSONI, Arber. (Pl. 9. fig. 34.)

Sporophylls attached.

1916. *Lepidostrobus Jacksoni*, Arber, in Phil. Trans. Roy. Soc. Ser. B, vol. ccviii. p. 147, pl. 4. fig. 19.

Diagnosis.—Cone of medium size, stalked, more or less club-shaped. Lower portion of sporophylls broad, scale-like, distal extremities prolonged as very narrow, elongated appendages, 4 mm. or more in length.

Remarks.—The type-specimen is refigured on Pl. 9. fig. 34, natural size. It has a length of 6.1 cm., and measures 2 cm. across at the apex, the broadest part. It contracts rather suddenly at the base. Only a portion of the lamina is seen, the lower part being broad but suddenly contracted above into long awn-like prolongations.

Type. No. 3250. Carbon. Plant Coll., Sedgwick Museum, Cambridge.

Distribution. Middle Coal Measures.

Coalfield :—South Staffordshire.

LEPIDOSTROBUS (?) SPINOSUS, Kidst. (Pl. 9. fig. 35.)

Sporophylls attached.

1838. *Lepidostrobus* sp., Brongn., Hist. Végét. Foss. vol. ii. p. 49, pl. 22. figs. 2, 3, & 8.

1888. *Lepidostrobus spinosus*, Kidston, in Trans. Roy. Soc. Edinb. vol. xxxiii. p. 396.

1893. *Lepidostrobus* (?) *spinosus*, Kidston, in Trans. Roy. Soc. Edinb. vol. xxxvii. pt. 2, p. 341, pl. 2. fig. 7, pl. 3. figs. 11 & 12.

Diagnosis.—Cone oblong and tapering to its blunt apex ; bracts lanceolate, acute, single-veined, adpressed, rigid ; external extremities of sporangia rhomboidal (Kidston, 1893).

Remarks.—The sporophylls of this rare type are very incompletely known. From Brongniart's figure it would appear that, as in *L. Jacksoni*, the laminae are distally contracted into narrow spines. The characters of the pedicel and the proximal portions of the lamina, which appear to differ from those of *L. Jacksoni*, are, however, obscure or unknown, and until these can be studied the specific value of this fossil must remain doubtful.

Kidston's type-specimen is refigured on Pl. 9. fig. 35, natural size.

Type. In Dr. Kidston's Collection, Stirling.

Distribution. Lower to Upper Coal Measures.

Upper Coal Measures.

Coalfield :—Radstock—Bristol.

Lower Coal Measures.

Coalfield :—Ayrshire.

EXPLANATION OF THE PLATES.

All the figures are from photographs by Mr. W. Tams of Cambridge; unless otherwise stated, the specimens figured are in the Sedgwick Museum, Cambridge. The numbers given refer to the Carboniferous Plant Collections in that Museum.

PLATE 8.

- Fig. 1. *Lepidostrobus variabilis*, Lindl. & Hutt. Middle Coal Measures. Wingham Boring, Kent. No. 2242. (Nat. size.)
- Fig. 2. *L. variabilis*, Lindl. & Hutt. Middle Coal Measures. Wingham Boring, Kent. No. 2242. ($\times 2$.)
- Fig. 3. *L. variabilis*, Lindl. & Hutt. Middle Coal Measures. Bishopsbourne Boring, Kent. No. 3201. (Nat. size.)
- Fig. 4. *L. brevifolius* (Lesq.). Upper Coal Measures. Upper Conygre Pit, Timsbury, Somerset. No. 1249. (Nat. size.)
- Fig. 5. *L. brevifolius* (Lesq.). Upper Coal Measures. Upper Conygre Pit, Timsbury, Somerset. No. 1249. ($\times 2$.)
- Fig. 6. *L. brevifolius* (Lesq.). ? Radstock, Camerton. No. 1266.
- Fig. 7. *L. brevifolius* (Lesq.). Upper Coal Measures. Upper Conygre Pit, Timsbury, Somerset. No. 1250. (Nat. size.)
- Fig. 8. *L. brevifolius* (Lesq.). Upper Coal Measures. Upper Conygre Pit, Timsbury, Somerset. No. 1257. (Nat. size.)
- Fig. 9. *L. hastatus* (Lesq.). Transition Coal Measures. Bishopsbourne Boring. No. 3147. (Nat. size.)
- Fig. 10. *L. hastatus* (Lesq.). Upper Coal Measures. Coal Pit Heath, near Bristol. No. 2069. (\times nearly 2.)
- Fig. 11. *L. intermedius* (Lindl. & Hutt.). Middle Coal Measures. Digby Clay Pit, Kimberley, Notts. No. 4014. (Nat. size.)
- Fig. 12. *L. intermedius* (Lindl. & Hutt.). Middle Coal Measures. Brindsley Clay Pit, Langley Mills, Notts. No. 4015. (Nat. size.)
- Fig. 13. *L. intermedius* (Lindl. & Hutt.). Lower Coal Measures. Trowell Coll., Notts. No. 4016. (Nat. size.)

- Fig. 14. *L. lanceolatus* (Lindl. & Hutt.). Radstock, Somerset. British Museum. V. 2944. (Nat. size.)
- Fig. 15. *L. lanceolatus* (Lindl. & Hutt.). Transition Coal Measures. Stone Hall Boring, Kent. No. 2415. (Nat. size.)
- Fig. 16. *L. lanceolatus* (Lindl. & Hutt.). Coal Measures (? Pennant Grit). Ricket's Head, Pembroke. No. 2904. (Nat. size.)
- Fig. 17. *L. lanceolatus* (Lindl. & Hutt.). Transition Coal Measures. Stone Hall Boring, Kent. No. 2417. (\times nearly 2.)
- Fig. 18. *L. longibracteatus* (Prestw.). British Museum, Natural Hist. Type-specimen [V. 3627]. Fig. 18A (Nat. size); Fig. 18B, cone (\times 2).
- Fig. 19A. *L. longibracteatus* (Prestw.). British Museum, Natural Hist. Type-specimen, V. 6344 (Nat. size); Fig. 19B, counterpart of type-specimen, V. 3626 (Nat. size).
- Fig. 20. *L. major* (Brongn.). Upper Coal Measures. Coal Pit Heath Colliery, near Bristol. No. 2076. (Nat. size.)

PLATE 9.

- Fig. 21. *L. major* (Brongn.). Upper Coal Measures. Bishop Sutton Colliery, Somerset. No. 3830. Pedicel (\times 3) to show network.
- Fig. 22. *L. minor* (Goode). Coal Measures (? Pennant Grit). Ricket's Head, Pembroke. No. 2902. (Nat. size.)
- Fig. 23. *L. minor* (Goode). Coal Measures (? Pennant Grit). Ricket's Head, Pembroke. No. 2903. (Nat. size.)
- Fig. 24. *L. minor* (Goode). Middle Coal Measures. Woodnesborough Boring, Kent. No. 2448. (Nat. size.)
- Fig. 25. *L. minor* (Goode). Middle Coal Measures. Maydensole Boring, Kent. No. 2295. (Nat. size.)
- Fig. 26. *L. Moyseyi*, sp. nova. Middle Coal Measures. Newthorpe Clay Pit, Notts. No. 4018. (Nat. size.)
- Fig. 27. *L. Moyseyi*, sp. nova. Newthorpe Clay Pit, Notts. No. 4018. (\times nearly 2.)
- Fig. 28. *L. radians*, Schimp. Coal Measures, ? Barnsley. No. 67. (Nat. size.)
- Fig. 29. *L. radians*, Schimp. Coal Measures, ? Barnsley. No. 78. (Nat. size.)
- Fig. 30. *L. radians*, Schimp. Coal Measures, ? Barnsley. No. 81. (Nat. size.)
- Fig. 31. *L. radians*, Schimp. Coal Measures, ? Yorkshire. No. 65. (Nat. size.)
- Fig. 32A. *L. triangularis* (Zeiller). Shipley, Notts. Moysey Collection. No. 3976. (Approximately nat. size.)
- Fig. 32B. Lower part of other half of same nodule as fig. 32A, showing some detached sporophylls. (Nat. size.)
- Fig. 33. *L. triangularis* (Zeiller). Detached sporophyll from Holly Hill. No. 201, Sir Charles Holcroft Collection, Geol. Dept., University of Birmingham. (Nat. size.)
- Fig. 34. *L. Jacksoni*, Arber. Between Bottom and New Mine Coals, Pouk Hill, Walsall. No. 3250. (Nat. size.)
- Fig. 35. *L. (?) spinosus*, Kidston. After Kidston, Trans. Roy. Soc. Edinb. vol. xxxvii. pt. 2, 1893: "On the Fossil Plants of the Kilmarnock Coal Fields," pl. ii. fig. 7. (Nat. size.)



1.



2 (x2).



3.



4



10 (x2).



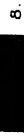
5 (x2).



6



7



8.



11.



13.



14.



15.



16.



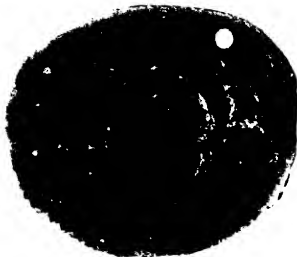
12.



17 (x2).



20.



19^A



18^B (x2).



18^A



19^B

LEPIDOSTROBUS.



21 (x3)



25.



26.



31.



22.



23.



27 (x2).



28.



24.



29.



35.



32.



33.



34.



32A

W Tams photo.

Huth coll

LEPIDOSTROBUS

II. LEPIDODENDRON LYCOPODIODES, Sternb., *L. OPHIURUS*, Brongn., and *L. LORICATUM*, *sp. nova*.

1. INTRODUCTION.

In the course of time, as the study of impressions of Coal-measure plants progresses, it has sometimes happened that doubts have arisen as to the exact nature of well-known species, which hitherto have been accepted almost without question. At first a mere suspicion arises as to whether such and such a plant is really identical with some ancient type in particular, and as to what exactly are the characters peculiar to it by which it is to be distinguished from other somewhat similar but probably distinct forms. Such suspicion may increase until a stage of uncertainty is reached. Or, again, it may be borne in on the worker, as he comes to have access to an ever-increasing range of materials, that confusions have arisen between somewhat similar but perhaps distinct species. At length a time is reached when it is necessary to set these doubts at rest by means of detailed re-examinations of the particular plants in question.

In the present notes I propose from time to time to give the results of such critical revisions as have seemed to me necessary as the result of many years' taxonomic experience of Coal-measure plants.

In the present note I deal with two of our Coal-measure species of *Lepidodendron*—*L. lycopodioides*, Sternb., and *L. ophiurus*, Brongn.,—both of very common occurrence, and also with a third type, which it is proposed here to term *L. loricaum*, *sp. nova*.

It appears to me that *L. ophiurus* has been largely confounded with *L. lycopodioides*, Sternb., and *vice versa*. Yet I hope to be able to show here that no grounds for such a confusion exist.

Two facts of importance may first of all be emphasised here. The first of these is that the only characters which are of any critical value as a means of discriminating species of *Lepidodendroid* stems are those exhibited by specimens showing the true external features of the leafless stems in question. This fact is, of course, widely recognised among palaeobotanists, but at the same time the opinion appears to be widely held that even specimens in which only the decorticated or subepidermal characters are exhibited can also sometimes be determined specifically. Or, again, it is urged that shoots entirely clothed with leaves can be identified. With these conclusions I am unable to agree (cf. 26. p. 150). I reject specific conclusions founded on such evidence.

Secondly, there appears still to be a considerable confusion as to the detailed morphology of the persistent leaf-armour of such stems, the units of which, in the leafless stems, are best described as leaf bases, though some prefer the term "leaf cushions." The matter is also frequently complicated by

the effects of crushing before or since preservation and by growth-changes which took place after the leaves were shed but before fossilisation. These questions are worthy of re-examination on a broad comparative basis not confined to a few species, and involving the study of a large suite of materials. I do not propose to enter into this complicated subject here, except in regard to a single point in connection with the leaf scar, which has a particular significance in the case of the species of *Lepidodendra* which are here particularly in question. According to my view, the leaf scar is that portion of the leaf base which marks the point of the actual union of the part of the leaf which was normally and naturally shed, when it had reached a particular stage in its development, with that part of the leaf which remained permanently attached to the shoot.

The sole characters which can be made use of in discriminating species of Lepidodendroid stems relate to the size, shape, and general characteristics of the leaf base as a whole and that particular region of the leaf base which we term the leaf scar. In the majority of British and Westphalian species, as is well known, the leaf scar is a perfectly definite area, usually clearly marked and more or less rhomboidal or triangular in shape. On well-preserved examples of the outer surface of the leaf bases, the prints of the vascular trace and the parichnos can usually be clearly distinguished within the leaf scar. In some, but not all, species, subparichnoid prints may occur beneath the leaf scar. Species of *Lepidodendron*, however, vary among themselves as regards the exact size and shape of the leaf scar and its position on the leaf base.

But the point which I wish to emphasize here is that, in at least one British species, the leaf scar is of an entirely different nature. It is not a superficial area, but a mere slit, transverse, more or less curved, and exhibits no prints comparable to the leaf trace and parichnoid prints of the more typical leaf scars.

It may be recalled that exactly the same phenomenon is met with in the Palæozoic genus *Cordaites* (12. pl. 27). Here, in perhaps the majority of cases, the leaf scar is very short, slit-like, and non-print-bearing. But other cases occur in which the leaf scar has a considerable height as well as breadth, and here the row of leaf-trace prints may be often seen.

In the case of *L. ophiurus*, Brongn., and *L. lycopodioides*, Sternb., which seem to me to have been considerably confused, the form of the leaf scar is alone sufficient to distinguish the species. *L. ophiurus* has, as I hope to show here, a superficial well-marked triangular scar, whereas *L. lycopodioides* has a mere slit. I commence by a re-examination of the characters of these two species, since here clearly lies the root of the difficulty.

It is a curious fact that, although both these species are such common plants in the Coal Measures of Britain and on the Continent, they have been comparatively rarely figured.

I now propose to instance the figured examples of these plants which have been already published, whether correctly or incorrectly assigned, with critical notes on each figure, and afterwards to add diagnoses founded on these and other specimens.

2. *LEPIDODENDRON LYCOPODIOIDES*, Sternb.

(Pl. 10. figs. 1-9 ; Pl. 11. figs. 10-17 ; Pl. 12. figs. 18-22.)

Revised synonymy of *Lepidodendron lycopodioides*, Sternb. :—

1820. *Lepidodendron dichotomum*, Sternb., Vers. Darstell. Flora Vorwelt, pt. 1, p. 23, pls. 1, 2.
 1821. *Lepidodendron lycopodioides*, Sternb., Vers. Darstell. Flora Vorwelt, pt. 2, pp. 26, 31, pl. 16. figs. 1, 2, & 4.
 1821. *Lepidodendron selaginoides*, Sternb., *ibid.* pt. 2, pp. 26, 31, pl. 16. fig. 3; pl. 17. fig. 1.
 1828. *Lycopodiolites selaginoides*, Bischoff, Kryptogam. Gewachse, p. 117, pl. 13. figs. 4-5 (copy of Sternberg's figures).
 1833 34. ? *Lepidodendron selaginoides*, Lindl. & Hutt., Fossil Flora, vol. ii. pl. 113.
 1833 34. *Lepidodendron elegans*, Lindl. & Hutt., *ibid.* vol. ii. p. 118.
 1838. *Lepidodendron* sp., Brongn., Hist. Végét. Foss. vol. ii. pl. 16. figs. 1-3 (copy of Sternberg's figures).
 1858. *Lepidodendron Sternbergii*, Buckland, Geol. & Mineral. London, 3rd Edit. vol. i. p. 432; vol. ii. p. 91, pl. 75 (copy of Sternberg's figure).
 1878 79. *Lepidodendron lycopodioides*, Zeiller, Explic. Carte Géol. France, vol. iv. pt. 2, p. 111, pl. 171. fig. 1.
 1879-80. *Lepidodendron lanceolatum*, Lesq., Coal Flora Pennsylv. p. 369, pl. 63. figs. 3-5.
 1886 88. *Lepidodendron lycopodioides*, Zeiller, Flore Foss. Bass. Houill Valenciennes, p. 464, pl. 69. figs. 2-3, pl. 70. fig. 1.
 1888. *Lepidodendron lanceolatum*, Kidston, in Trans. Roy. Soc. Edinb. vol. xxxiii. p. 394, pl. 27. fig. 5, pl. 28. figs. 3-4.
 1903. *Lepidodendron lycopodioides*, Arber, in Quart. Journ. Geol. Soc. vol. lix. p. 12, pl. 2. fig. 5.
 1903. *Lepidodendron lycopodioides*, Kidston, in Trans. Roy. Soc. Edinb. vol. xl. pt. 4, p. 795.
 1903. *Lepidodendron lycopodioides*, Arber, in Mem. & Proc. Manchester Lit. & Phil. Soc. vol. xlviii. No. 2, p. 18, and text-fig. on p. 19.
 1904. *Lepidodendron ophiurus*, Zalessky, in Mém. Com. Géol. St. Pétersbourg. N.S. Livr. 13, pp. 23 & 95, pl. 5. fig. 3.
 1909. *Lepidodendron lycopodioides*, Arber, Fossil Plants, p. 67, and fig. on p. 9.
 1910. *Lepidodendron ophiurus*, Renier, Doc. Étude Pal. Terr. Houill. p. 13, pl. 6. figs. b & c.
 1912. *Lepidodendron lanceolatum*, Arber, in Phil. Trans. Roy. Soc. ser. B vol. ccii. p. 250, pl. 12. fig. 14.
 1914. *Lepidodendron lanceolatum*, Arber, *ibid.* ser. B, vol. cciv. p. 402, pl. 28. fig. 26.

Remarks on the Specimens previously figured.

Of the figures of Sternberg's types (1821) of *L. lycopodioides*, only figs. 2 and 4 of pl. 16 are important. Fig. 1 of the same plate represents a

decorticated condition. In the case of fig. 2, the leaf bases are smooth and much longer than broad. There is no definite leaf scar, but apparently a slight, very impersistent keel occurs in the upper part of the base. Fig. 4 may be neglected entirely. It is highly suspicious on the score of accuracy and is probably entirely misleading.

Turning now to the types of the same author's *L. selaginoides* (pl. 16. fig. 3 ; pl. 17. fig. 1) one finds simply two leafy stems, which, in those parts which are leafless, are more or less decorticated. The identity of *L. selaginoides*, Sternb. with *L. lycopodioides*, Sternb., is, I believe, now generally admitted (15. p. 137 ; 16 p. 795). I do not propose to discuss this matter further, since I regard it as proved that the two forms have been found in organic continuity and are therefore one and the same plant. The specimens figured by Sternberg under the name *L. dichotomum* a year earlier than the above types, have long been a puzzle to palaeobotanists and will probably continue to be a stumbling-block. I do not propose to enter in detail into previous opinion as to their nature, except to add that most authorities have regarded them as distinct from both *L. lycopodioides* and *L. ophiurus* and as the type of a distinct species (*L. dichotomum*) which was first fully figured by Zeiller. My view is that the specimens figured by Sternberg, 1820, on plates 1 & 2 (except the lower left-hand figure on plate 2), are all, so far as one can judge from the leaf bases, simply typical *L. lycopodioides*. I regard them as distinct from the specimen figured under the same species by Sternberg in 1838 on plate 68. fig. 1 of the 7th part of his 'Versuch.' This plant I propose to re-name *L. loricaum* (see p. 201).

Omitting Bischoff's figure, which is simply a copy of one of Sternberg's, we next reach Lindley and Hutton's examples figured in the second volume of their 'Fossil Flora.' While I am in some doubt about their plate 113, since the leaf bases are either decorticated or imperfectly represented, the plate 118 of the same authors appears to me to represent typical leaf bases of *L. lycopodioides*. Of Zeiller's figures, one example figured in both places is decorticated. The figs. 3, 3A of the Valenciennes Flora are, however, very important, as the earliest clear example of the characters of the leaf bases of this species. It is obvious that this great authority held the same view which I hold as to the true nature of this species. In place of a leaf scar one finds a crescentic, somewhat triangular slit, while the lower part of the keel of the leaf base has small transverse notches. One of the figures of this plant which I published in 1903 from the Lancashire coalfield may be slightly decorticated, while the other from the Cumberland field, which appeared in the same year and was re-figured on a larger scale in 1909, is typical. The transverse ridges on the keel are here prominent.

With regard to Zalesky's figure (1904) it is a little difficult without seeing the specimen to feel sure as to the species which it represents, though the leaf scar appears to me to agree with *L. lycopodioides*. The keel,

however, does not appear to be ridged. The most recent figures by Renier (1911) are also similar.

Notes on the Examples of L. lycopodioides here figured.

(The numbers refer to specimens in the Carboniferous Plant Collections,
Sedgwick Museum, Cambridge.)

As in other species of *Lepidodendron*, the leaf bases of this type differ greatly in size and shape, according to the age of the branch.

No. 3205. One of the specimens of this species, with the largest leaf bases with which I am acquainted of any from this horizon, is shown, natural size, on Pl. 10. fig. 1 and enlarged in fig. 2. This is a specimen from the Middle Coal Measures of the Bishopsbourne Boring, Kent, at 2513 ft. The leaf bases here measure 14.5 mm. long by 7 mm. broad. They are much less crushed than is usually the case. The lateral angles are rounded, the apex is somewhat obtuse, and the lower extremity attenuated, straight or slightly bent. The leaf scar is a transverse slit situated very high up. As is so often the case in regard to this species, the carbon of the leaf base is extremely brittle and is liable to flake off, especially in the neighbourhood of the leaf scars. Sometimes the absence of a small triangular piece of carbon in this region simulates, and may be mistaken for, a leaf scar. The lateral lines arising from the leaf scar are long and extend downwards to or just beyond the lateral angles of the base. The keel below the leaf scar is ornamented by numerous transverse ridges, especially in the lower part of its course.

No. 2754. The leaf bases of another specimen from Bond's Main Colliery, Temple Normanton, Derby (Middle Coal Measures), are illustrated on Pl. 10. fig. 3, natural size. Here the carbonaceous film has flaked off in the neighbourhood of the scar—a characteristic feature. These leaf bases measure about 14 mm. in length and 5 mm. in breadth. They are very little compressed, and the lateral lines are clear. The keel is faint or absent, and the ornamentation is slight.

No. 107. We pass now to branched examples still bearing some leaves attached. Fig. 4, Pl. 10, shows the leaf scars of such a specimen from Toronley Colliery (coalfield unknown), natural size, and Pl. 10. fig. 5, the same enlarged. The leaf bases are here 7 or 7.5 mm. long and about 3 mm. across. In most cases they are slightly decorticated by the flaking off of the carbon. The lateral lines are clear. The keel is faint, but the ornamentation consists of round or oval conspicuous projections.

No. 927. Figs. 6 & 7, Pl. 10, represent a specimen from the Middle Coal Measures of Flimby, Cumberland, which has several times been figured. The leaf bases here are very broad, quadrate, almost square, measuring 6.5 × 5.5 mm. The angles are nearly all equal. The leaf scar is almost, if not

quite, terminal. The lateral lines are faint. The keel is faintly ornamented, especially on the lower part.

No. 950. A transition from the quadrate to the fusiform types above discussed is seen in the leaf bases figured, enlarged three times, on Pl. 10. fig. 8. Here the bases measure 6 mm. long and 3.5 mm. broad. The leaf scar here has the form of an upright slit. The ornamentation is conspicuous.

No. 68. An example with small leaf bases from the Middle Coal Measures of Barnsley is figured on Pl. 10. fig. 9, enlarged three times. The leaf bases here measure 4 mm. long and 2 mm. broad. The carbon has flaked off most of the regions around the leaf scar. The keel is very faint and no ornamentation is distinguishable.

No. 106. Since it appears to have been held that the normal conditions of the leaf scar in this species is due to an accidental and unnatural fracture of the leaf, it may be well to figure an example of such an occurrence for comparison. In fig. 10, Pl. 11, some broken bases of leaves fractured unnaturally are seen enlarged. It will be noticed that the appearance in this case is quite different from those figured above, in which the leaf base, as left attached to the stem by the natural fall of the leaf, is exhibited.

Further, since this species commonly occurs in various stages of decortication, due as we have seen in the case of carbonaceous impressions to the tendency of the carbonaceous film to flake off, it may be well to figure here some examples in which the decortication is comparatively slight.

No. 3475. On Pl. 11. fig. 11, some leaf bases from the Middle Coal Measure of Bentley, South Staffordshire, are seen slightly enlarged. This is an impression in intaglio, and probably slightly decorticated. The leaf scar is here a crescentic ridge, inside the angle of which a short vertical ridge occurs. The leaf bases are here exceptional in being separated by double bands of bark.

This species is very common in ironstone nodules and bands in the Middle Coal Measures of the Midlands, usually occurring as intaglio impressions, more rarely as casts.

My experience of these fossils leads me to believe that they are almost always more or less decorticated, though the leaf bases are rarely crushed.

No. 754. Fig. 12, Pl. 11, shows (in relief) natural size leaf bases from an ironstone cast of this species from the Middle Coal Measures at Bradford, Yorkshire. In the position of the leaf scar a small pit occurs, triangular in form (isosceles with a narrow base). The keel is very strong, but shows no ornamentation.

No. 755. Fig. 13, Pl. 11, is from a wax cast of another specimen from the same locality, this time preserved in intaglio. The irregular area around the position of the leaf scar reminds one of the appearance of many

carbonaceous casts in which the carbon film has flaked off to a considerable extent.

No. 3568. Leaf bases from a wax cast of an intaglio impression from the Ten-foot Ironstone of the famous locality of Cosely, South Staffordshire, are shown on Pl. 11. fig. 14, enlarged twice.

This is a branch of small diameter with leaves still attached at the sides. The upper leaf bases are perfect, the lower are very imperfect in the neighbourhood of the leaf scar.

Nos. 3249 & 1475. Two stages in decortication of carbonaceous impressions are also figured in Pl. 11. fig. 15 and fig. 16. The former is the less decorticated.

The Case for Lepidodendron lanceolatum, Lesq.

In 1879–80 Lesquereux figured specimens from Pennsylvania under the new specific name, *L. lanceolatum*, Lesq. In 1888 Kidston recognised this type in the flora of the Upper Coal Measures of the Radstock coalfield and adopted Lesquereux's name. More recently the present author has figured other examples from the Forest of Dean and Wyre Forest fields, and from both the Upper and Transition Coal Measures. This species is, however, unknown in the Middle Coal Measures or, indeed, from any horizon lower than the Transition series. The references to the above literature will be included in the synonymy of *L. lycopodioides* given in the present paper.

As to the identity of the British specimens, figured by Kidston and myself, with Lesquereux's plant, in the absence of examples for comparison from the Pennsylvania coalfield, one cannot feel absolute certainty, though I regard it as extremely probable that they are identical. A critical re-examination of these species of *Lepidodendra* has, however, convinced me that the British plant, hitherto assigned to *L. lanceolatum*, is nothing more nor less than *L. lycopodioides*, Sternb. The leaf bases and the leaf scars are identical with those of that species. The only point in which I can find any difference is in the size of the leaf bases in certain specimens which are much larger than those of any example of *L. lycopodioides*, Sternb., known to me from the Middle Coal Measures. This, however, is immaterial, for examples of more slender specimens with leaf scars comparable in size to *L. lycopodioides* occur in abundance. I figure here three specimens from the Upper and Transition Coal Measures which vary in size only.

No. 1624. On Pl. 11. fig. 17 is shown part of a stem from the Upper Coal Measures of the Forest of Dean, some of the leaf bases of which are represented in Pl. 12. fig. 18, enlarged three times. This is one of the specimens with the largest leaf bases known to me. They measure almost 17 mm. in length by 4 mm. in breadth. The preservation is particularly perfect, though here, as in other cases, the carbonaceous film tends to flake

off, especially in the neighbourhood of the leaf scar. The keel in this instance is rather faint, except just below the leaf scar, but the ornamentation can be recognised.

No. 1986. Enlarged leaf bases of another example from the same field are seen on Pl. 12. fig. 19 ($\times 3$). Here the leaf bases are 11 mm. long. The keel is also faint, but the ornamentation is clear.

No. 2507. Leaf bases of an example from a lower horizon, Transition Coal Measures in the Wyre Forest, are shown enlarged on Pl. 12. fig. 20. They measure 8 mm. in length. The keel is faintly recognisable in some cases, but hardly at all in others.

No. 2066. On fig. 21, Pl. 12, a few leaf bases are shown, natural size, from an example from the Upper Coal Measures of the Bristol coalfield. The leaf bases here are very elongate in proportion to their breadth, measuring 13.5 mm. long and 3 mm. broad. No keel or ornamentation can be recognised. In other specimens with similar leaf bases 10 mm. long, the shoots are branched and still leafy in places.

No. 1625. This is a specimen of a more slender branch with some leaves still attached. The leaf bases are shown on Pl. 12. fig. 22, enlarged three times. They measure 7 mm. in length by 3 mm. across. The keel is very faint, if present, but the ornamentation is clear. This example is derived from the Upper Coal Measures of the Forest of Dean. Otherwise it agrees with the specimens of *L. lycopodioides* from lower horizons, already described.

I may further add that I now think that the specimen from the Transition Coal Measures of South Staffordshire recently figured by me (2. p. 145, and text-fig. 3) as *Lepidodendron* sp. is probably an old age stage of *L. lycopodioides*.

*Figured Examples incorrectly or doubtfully identified with
L. lycopodioides.*

I turn now to criticise certain specimens attributed to *L. lycopodioides*, incorrectly as it appears to me, or in some cases doubtfully.

The synonymy given by Schimper (25. ii. p. 19) seems to me to be a confusion between *L. lycopodioides* and *L. ophiurus* and yet other species, and is thus best ignored. The specimens figured on plate 51 of that author's 'Traité' alone appear to belong to the former species. This imperfect synonymy is no doubt the initial cause of the confusion which has since arisen with regard to these fossils.

List of synonyms of this species have been published by Zeiller (27. p. 464) and Kidston (16. p. 795).

With regard to the former's list I should omit the references to Renault and Brongniart's figures as relating to *L. ophiurus*. The other examples, including those then figured by Zeiller, really do represent the true *L. lycopodioides*.

Kidston's most recent synonymy (16. p. 795), which, however, pre-dates the proposal to establish *L. simile*, Jongmans, also contains the above reference to Renault, but not to Brongniart. Many of the figures here referred to simply relate to leafy branches, in which the leaf-base characters cannot be distinguished. This is the case with Kidston's own figure published in 1902 and those of Foistmantel (1875).

Diagnosis of L. lycopodioides, Sternb.

Leaf bases approximate, separated by slight grooves, rhomboidal, somewhat prominent, usually longer than broad, very varied in size, ranging up to 17 mm. in length and 4 mm. in breadth, lateral angles rounded, upper and lower extremities usually straight, more rarely slightly bent, very acute.

Leaf scar a curved triangular or semi-lenticular slit, narrower than the leaf base and placed considerably above its centre, sometimes near the apex, at others some distance below it. From the lateral extremities of this slit, two lines or ridges curve obliquely downwards to meet the margin of the leaf base, at about the level of the lateral angles. A distinct but slight keel is present, both above and below the slit, though sometimes the keel is faint, the lower keel being usually ornamented by short and slight transverse ridges, especially in the lower part of its length. No sub-parichnoid prints occur below the leaf slit.

3. LEPIDODENDRON OPHIURUS (Brongn.).

(Pl. 12. figs. 23-26.)

Revised synonymy of *Lepidodendron ophiurus* (Brongn.):—

- 1822. *Sagenaria ophiurus*, Brongn., in Mém. Mus. Hist. Nat. vol. viii. p. 227, pl. 15 (4).
fig. 1 a-b.
- 1828. *Lycopodiolites Ophyurus*, Bischoff, Kryptogam. Gewächse, pp. 117, 131, pl. 13.
figs. 6 a, 6 b.
- 1838. *Lepidodendron elegans*, Brongn., Hist. Végét. Foss. vol. ii. p. 35 (footnote), pl. 14.
- 1838. *Lepidodendron gracile*, Brongn., *ibid.* pl. 15.
- 1848. *Lepidodendron ophiurus*, Sauveur, Végét. Foss. Terr. Houill. Belgique, pl. 59.
figs. 2 a, 2 b.
- 1878-79. *Lepidodendron gracile*, Zeiller, Explic. Carte Géol. France, vol. iv. pt. 2, p. 112,
pl. 172. fig. 2.
- 1882. *Lepidodendron lycopodioides*, Renault, Cours Bot. Foss. vol. ii. p. 14, pl. 5. fig. 8.
- 1886-88. *Lepidodendron ophiurus*, Zeiller, Flore Foss. Bass. Houill. Valenciennes,
p. 458, pl. 68. figs. 1-6.
- 1903. *Lepidodendron Glincanum*, Kidston, in Trans. Roy. Soc. Edinb. vol. xl. p. 762,
pl. 2. figs. 20, 21; pl. 4. figs. 37-40.
- 1904. *Lepidodendron ophiurus*, Zalessky, in Mém. Com. Géol. St. Pétersbourg, N. S.
Liv. 13, pp. 23, 95, pl. 5. figs. 1, 2, 4, 6.
- 1906. *Lepidodendron ophiurus*, Fischer, in Potonié Abbild. und Beschr. Foss. Pflanz.
Lief. 4, No. 73 with fig.
- 1912. *Lepidodendron simile*, Vernon, in Quart. Journ. Geol. Soc. vol. lxviii. p. 621,
pl. 57. fig. 7.

Remarks on the Specimens previously figured.

Brongniart's type (1822), although not then described, was clearly figured, and the illustration on plate 15. fig. 1 *b* of that memoir can leave little doubt as to the specific nature of the specimen. The leaf bases are here rather small with a well-marked keel both above and below the leaf scar. The keel is not ornamented. The leaf scar is situated considerably above the centre of the base, and is here shown as being rhomboidal in form with a single central print. Leaves are also seen still attached to some of the leaf bases.

The same author's *L. elegans* and *L. gracile* figured in 1838, again without description, show precisely similar leaf bases, with the exception that in some cases the keel below the leaf scar is slightly but clearly notched, and that prints are only very rarely indicated within the leaf scar. The shape of the scar is, however, perfectly definite.

Sauveur's fig. 2 *b* (1848) agrees very closely with the type, but again the species remained undescribed. The first description of this species was published in 1879 by Zeiller. In the case of the cone-bearing specimen figured by this author, no enlarged drawing of the leaf bases is given, but it is clear that the leaf scar was more or less triangular in form and not slit-like.

Zeiller (1879), under the name of *Lepidodendron gracile*, L. et H., gives the first description of the plant which we here regard as *L. ophiurus*. This description, somewhat abbreviated, is as follows :—Branches slender, cushions rhomboidal, rather prominent, 3-4 times as long as wide, extremities acute, lateral angles rounded. Leaf scar placed in the uppermost quarter of the axis of the cushion, rather high than broad, with the upper angle rounded. Keel very clear, with only some very small, scarcely distinct, transverse folds. Lines of decurrence arising from the lateral angles of the leaf scar. Vascular print indistinct, placed towards the centre of the leaf scar.

Renault's figure, published in 1882 and referred to *Lepidodendron lyropodioides*, Sternb., is no doubt one of the earlier stages in the confusion which has arisen between these two species. The leaf bases agree with those of Brongniart's later figures, except that the keel is perhaps more strongly notched than in any examples previously figured. The usual prints of the leaf scar, although scarcely indicated in Renault's drawing, are duly noticed in his diagnosis. We now reach the most important figures of this plant which have yet appeared, the illustrations so well described by Zeiller in 1886-88. Reserving a few remarks on his synonymy of this species for the moment, we may notice that Zeiller figures a definite leaf scar, which is also fully described in the text. It has a single central print. The keel of the leaf base is not ornamented.

Of the specimens attributed to this species by Zalesky in 1904, the majority are correctly referred, though one or two appear to be examples of

L. lycopodioides, or perhaps of other species also. Passing by Fischer's contribution, the most recent figure of this plant is that given by Vernon under the name *Lepidodendron simile*, Jongmans.

Several examples of the cones of this species have been figured by Nathorst, Kidston, and others, but I do not propose to discuss these here, as I am solely concerned with the vegetative shoots of this plant. I would, however, point out that those recently attributed by Kidston (18. pl. 11. figs. 2 & 3) belong, in my opinion, to *L. lycopodioides*.

Notes on the Examples of L. ophiurus here figured.

No. 131. A portion of an example of this species with rather large leaf bases is figured on Pl. 12. fig. 23, natural size, and in fig. 24, enlarged. The leaf bases vary from 7.5 to 10 mm. in length, and average about 5 mm. across at their widest point. The leaf bases are separated by double bands of bark, and the lateral angles are somewhat rounded, though still distinctly angular. The upper and lower extremities are straight or slightly curved. The leaf scar lies above the centre and is, as is usually the case, very clearly marked. It occupies almost the whole width of the rib. It bears the three usual prints, often rather faintly preserved. It is comparatively tall, the upper and lateral angles being acute, while the lower angle is very obtuse or somewhat concave. The lateral lines are short and not clearly marked. The keel is faint except at the very base, and the ornamentation is either absent or very faint. There are no sub-parichnoid prints.

No. 3472. In the specimen seen enlarged three times on Pl. 12. fig. 25, the leaf bases are much smaller. They measure 4 mm. in length by 2 mm. in breadth. There is only one print of the leaf scar visible and that is central. The keel is well marked and is without ornament.

No. 3478. Another example is shown enlarged three times on Pl. 12. fig. 26. This has quite small leaf bases, as is commonly the case among the leafy twigs of this species. Here they measure 3 mm. in length by 2 mm. or a little more in breadth. They are otherwise similar to those seen in the specimen last described, except that no prints can be seen of the leaf scar.

Figured Specimens incorrectly or doubtfully identified with L. ophiurus.

It may be noticed in passing that Schimper (25. ii. p. 19) overlooked or ignored Brongniart's *L. ophiurus*. The *L. elegans* and the *L. gracile* of Brongniart are referred by him to *L. Sternbergii*, Brongn., which I regard as an error.

With regard to Zeiller's list of synonyms published in 1888, I should merely reject as doubtful the references to Sternberg's *Lycopodiolites affinis* (1826, pt. 4, pl. 56. fig. 1), Lindley & Hutton's *Lepidodendron gracile* (1831, vol. i. pl. 9), and the same authors' *L. dilatatum* (1831, vol. i. pl. 7. fig. 2).

These specimens appear to me to be all decorticated and their specific attribution doubtful.

Dr. Kidston's most recent lists (18. p. 132) of synonyms of *L. ophiurus*, also contain the above references, which I should omit. There is, further, a more doubtful reference to Lindley and Hutton's *Lepidodendron Sternbergii* (1831, vol. i. pl. 4; 1834, vol. ii. pl. 112), as well as to figures of cones and leafy shoots of this species which are not under consideration here. Some of the former, as I have said, belong to *L. lycopodioides*.

The Case for Lepidodendron simile, Jongmans.*

In 1909, Jongmans (14. p. 174) published the following synonymy, and figured examples to which the new term *L. similis* (sic) was applied:—

1833-34. *Lepidodendron elegans*, Lindl. & Hutt. Foss. Flora, vol. ii. pl. 118.

1838. *Lepidodendron elegans*, Brongn., Hist. Végét. Foss. vol. ii. p. 35, pl. 14.

1878-79. *Lepidodendron lycopodioides*, Zeiller, Explic. Carte Géol. France, vol. iv. pt. 2, p. 111, pl. 171.

1882. *Lepidodendron lycopodioides*, Renault, Cours Bot. Foss. vol. ii. p. 14, pl. 5. fig. 8.

1886-88. *Lepidodendron lycopodioides*, Zeiller, Flore Foss. Bass. Houill. Valenciennes, p. 464, pl. 69, figs. 2-3; pl. 70. fig. 1.

This synonymy appears to me to represent a confusion between two distinct species.

The Brongniart and Renault figures are, as I have attempted to show here, examples of *L. ophiurus*.

On the other hand, Lindley and Hutton's plant and all the specimens here indicated as figured by Zeiller in 1878-79 and 1886-88 appear to me to be undoubtedly *L. lycopodioides*, Sternb.

In discussing this synonymy one is at a disadvantage, for, although something like ten years have passed since it was first put forward, and although Kidston (15. p. 137; 18. p. 134) has subsequently repeated it on several occasions, no diagnosis of Jongmans' species has ever been published. We have not been told what are the essential characters in which these particular plants are all supposed to agree, and how they differ from other related species. In fact, in view of the modern laws of nomenclature, it is doubtful whether Jongmans' name has, in the absence of a diagnosis, any scientific status whatever. Kidston has merely told us that the foliage of *L. lycopodioides* is distinct from that of the plants which he cites as *L. simile*, some of which, however, are *L. lycopodioides* pure and simple, according to no less an authority than the late Prof. Zeiller. With this view I quite agree, and I reject *L. simile*, Jongmans, as adding confusion to an already involved question.

* This is a MS. name of Kidston's, but this authority is ignored here since MS. names are best discarded. The specific name was first actually published by Jongmans, who thus became the author.

Diagnosis of L. ophiurus, Brongn.

Leaf bases approximated, separated by slight grooves, rhomboidal, prominent, always longer than broad, of small to medium size, 3–10 mm. long and 2–5 mm. wide, lateral angles rounded, but still angular, upper and lower extremities straight or more rarely slightly curved. Leaf scar clearly marked, situated considerably above centre of leaf base, occupying nearly its whole width, upper and lateral angles acute, lower angle very obtuse. From the lateral angles two lines descend sometimes to near the lower extremity of the leaf base, parallel to its contour and a short distance from its margin. Keel well marked or faint, usually without ornamentation, but sometimes with a few faint, short, transverse ridges. Keel above leaf scar prominent. Prints of the leaf scar of the usual type, rather faint, sometimes invisible, or only a central print to be seen.

4. LEPIDODENDRON LORICATUM, *sp. nova.*

(Pl. 13. figs. 27–37.)

Bound up with the preceding species, at any rate to some extent historically, is another type of stem usually known as *Lepidodendron dichotomum*, Sternb., or *L. dichotomum*, Zeiller. This plant I now propose, for reasons which will be found fully stated below, to transfer to a new species as *L. loricatum*, *sp. nova.*

Synonymy of *Lepidodendron loricatum*, *sp. nova* :—

1838. ? *Lepidodendron dichotomum*, Presl, in Sternberg, Vers. Darstell. Flora Vorwelt, pt. 7, p. 177, pl. 68. fig. 1.
 1878–79. ? *Lepidodendron dichotomum*, Zeiller, Explic. Carte Géol. France, vol. iv. pt. 2, p. 107, pl. 72. fig. 1.
 1886–88. *Lepidodendron dichotomum*, Zeiller, Flore Foss. Bass. Houill. Valenciennes, p. 446, pl. 67. fig. 1.
 1903. *Lepidodendron dichotomum*, Arber, in Mem. & Proc. Manchester Lit. & Phil. Soc. vol. xlviii. No. 2, p. 20, pl. 1. figs. 1 & 2.
 1904. *Lepidodendron dichotomum*, Zalessky, in Mém. Com. Géol. St. Pétersbourg, N. S. Livr. 13, p. 9, pl. 2. figs. 3, 5, 6; pl. 3. figs. 3, 5, 7–12; pl. 4. fig. 11.
 1912. *Lepidodendron dichotomum*, Arber, in Phil. Trans. Roy. Soc. ser. B, vol. ccii. p. 251, pl. 11. fig. 6.
 1914. *Lepidodendron dichotomum*, Arber, *ibid.* ser. B, vol. cciv. p. 402, pl. 29. fig. 36.

Remarks on the Specimens previously figured.

In the first part of Sternberg's 'Versuch,' published in 1820, the first three plates relate to a *Lepidodendron* which the author termed *L. dichotomum*. Neglecting the third plate, we have already shown that most of the figures of plates 1 & 2 of that work are, in our opinion, identical with the other specimens figured in the following year by the same author as *Lepidodendron lycopodioides*, Sternb. The latter name is thus, strictly speaking, a

synonym of *L. dichotomum*, but, as in the course of time it has become almost universally used to denote this particular fossil, it is nevertheless maintained as the accepted name for this species. It may be also noted that the figures of these two plates were re-named *Lepidodendron Sternbergii* by Brongniart in 1828 (4. p. 85). This, however, is an unnecessary complication which may be ignored.

The next step in the matter dates from 18 years later (1838), when Presl in the 7th part of the same 'Versuch' of Sternberg's (see above synonymy) figured a further specimen under the same name, *L. dichotomum* *. This illustration is small and possibly not very accurate, and considerable doubt has long existed as to what it really represents. My conclusions on this point are two-fold. Firstly, I am convinced that it is an entirely distinct plant from the specimens first figured as *L. dichotomum*. It is therefore obvious that it must receive a fresh name. Secondly, I am not satisfied that the specimens which Zeiller, Zalessky, and I have in more recent years figured under the name of *L. dichotomum* are the same plant as that shown in the later figure of Sternberg. They may be. This possibility is not ruled out of court, but until Sternberg's type, if still known, has been re-examined, the matter must remain doubtful. In any case, some new specific name must be applied to the more recent specimens, since the name *L. dichotomum* is inapplicable, quite apart from the question whether Sternberg's later figure does or does not represent the plant which occurs in Britain. I therefore propose the new species *L. loricatum* to include the more recent examples included in the above synonymy, beginning with Zeiller's figure. These specimens all appear to be a very homogeneous set and call for no further remarks here.

Notes on the Specimens of L. loricatum, sp. nova, here figured.

No. 2506. Beginning with the napiform types and those with the largest leaf bases, we turn to the specimen, part of which is figured natural size on Pl. 13. fig. 27 and enlarged twice in fig. 28.

The leaf bases are here slightly taller than broad, measuring 6 mm. one way and 5 mm. the other. The upper angle of the leaf base is very rounded, the lower prolonged and acute. The leaf scar is situated near the apex of the base and is prominent. It occupies about two-thirds the width of the base. All its angles are nearly equally acute, except the upper, which is so very broadly rounded as to be almost non-existent. The leaf scar prints are quite clear (fig. 28). The keel is faint.

No. 2470. An enlarged figure of part of another specimen from the Transition Coal Measures of Kent is seen on Pl. 13. fig. 29. This is similar

* The Presl names are all MS. and therefore are ignored. The authority is taken as Sternberg in all cases, since he actually published them.

to the last specimen, but the leaf bases are rather smaller, measuring 5 or 5.5 mm. in length and only 2.5 to 3 mm. in breadth. The upper angle of the base is also rather more pointed than in the last specimen. The leaf scar prints are particularly clear.

No. 959. Prominent leaf bases from another specimen from the Middle Coal Measures of Cumberland are seen enlarged on Pl. 13. fig. 30. These show the sub-imbricate arrangement of bases, the rounded upper angle, and apical leaf scar. The leaf bases are here as high as broad (5 mm.).

No. 3109. Part of a further specimen from the Transition Coal Measures of Kent is seen natural size on Pl. 13. fig. 31, and enlarged three times in fig. 32. The leaf bases here measure about 4 mm. each way. The leaf scar is clearly oblique and placed considerably below the angle of the leaf base, and nearly all its sides and angles are equal. There is no appearance of any keel.

No. 1645. Passing next to fusiform types, the specimen from the Upper Coal Measures of the Forest of Dean, figured on Pl. 13. fig. 33, natural size, and in fig. 34, enlarged twice, is a good example of a type with comparatively large leaf bases. They measure 10.5 mm. by 5 mm. across. The base is fusiform, with attenuated and sharp upper and lower angles. The leaf scar is set obliquely slightly above the centre of the base and occupies two-thirds of its breadth. The lateral and lower angles are sharp, but the upper is slightly rounded. The leaf-scar prints are clear. A keel is present, but is not very prominent, and has no ornamentation. There is no keel above the leaf scar.

No. 1953. Part of another specimen from the Upper Coal Measures of the Forest of Dean is shown enlarged on Pl. 13. fig. 35. The leaf bases here measure about 10 mm. by 4 mm. The leaf scar is prominent and the keel is well marked without ornamentation.

No. 3130. Another specimen from the Transition Coal Measures of the Kent Coalfield is seen on Pl. 13. fig. 36, natural size, and in fig. 37, enlarged three times. The leaf bases are here very long (7 mm.) in proportion to their breadth (1.5 mm.). The keel is very faint.

Figured Examples incorrectly or doubtfully identified with the Plant here termed L. loricaum, sp. nova.

Owing to the confusion which has arisen from the fact that Sternberg included at least two different plants under the name *L. dichotomum*, few, if any, of the synonyms previously published have any bearing on the fossil here under consideration. Schimper's (25. ii. p. 20) synonymy may be passed by as foreign to this question. Zeiller, who published the first good figures of the species here termed *L. loricaum*, includes a number of references which I should reject, especially the inclusion of Sternberg's

earlier figures (1820) assigned to *L. dichotomum* *. Thus Feistmantel's (8. pl. 32. figs. 1, 3, 5) figures of *L. dichotomum* appear to me to relate more probably to a species of *Lepidophloios*. Lindley and Hutton's *L. Sternbergii* (20. i. pl. 4) is a decorticated specimen and probably belongs to *L. lycopodioides*.

Among the specimens figured by Geinitz (9. p. 34, pl. 3. figs. 1-12) under the name *Sagenaria dichotoma* there are probably included representatives of more than one species. Several of the specimens, at any rate, are clearly indeterminable specifically and others are very doubtful. All that one can conclude is that, if any of them represent *L. loricatum*, it is probably figs. 8 and 12, but I am not convinced that this is the case. Turning next to Zalessky's synonymy, which includes several references common to Zeiller's which have just been criticised, we find also a comparison with Roehl's (23. pl. 8. fig. 6 ; pl. 11. fig. 2) figures of *L. dichotomum*, both of which appear to me to be probably distinct from *L. loricatum* as here defined. I should also be inclined to regard as distinct Ettingshausen's *L. brevifolium* (6. pl. 24. fig. 5 ; pl. 26. fig. 3) and also the Radnitz specimens attributed by the same author to *L. Sternbergii* (7. pl. 26. figs. 1, 2 ; pls. 27, 28). With regard to Sauveur's figures I should reject as indeterminable *L. minutum* (24. pl. 61. fig. 3), while *L. clathratum* (24. pl. 61. fig. 4) may be *L. ophiurus*, though this is uncertain.

Kidston's *L. Glincaum* (16. pl. 2. figs. 20, 21 ; pl. 4. figs. 37-40) appears to be *L. ophiurus*.

Diagnosis of L. loricatum, sp. nova.

Leaf bases approximate, separated by slight grooves, napiform and sub-imbricated or fusiform and non-imbricated, somewhat prominent, in napiform types as broad as high or slightly longer than broad, on an average about 5 mm. each way or sometimes 4 mm. or less in breadth ; in fusiform types twice as long as broad or even more, up to 10 mm. long and up to 5 mm. broad, lateral angles rounded, lower angle nearly always prolonged, upper angle broadly rounded or blunt and short in napiform types, acute and prolonged in fusiform types. Leaf scar situated at or below the upper limit of leaf base occupying the greater width or even the whole of the base, often set obliquely on the base, prominent, rhomboidal. Upper angle usually somewhat rounded, or all sides and angles nearly equal and acute. From the lateral angles two lines may diverge downwards and outwards, but soon merge in the margin of the leaf base ; these are often invisible. Prints of leaf scar three, the median being the most distinct. A punctate ligular scar occurs above the leaf scar. Sub-parichnoid scars always absent. Keel of

* These were re-figured by Bischoff and Brongniart and in the editions of Buckland (5. i. p. 432 ii. p. 91, pl. 75).

leaf base faint or often absent in napiform types, slight or fairly prominent in fusiform examples; rarely if ever occurring above the leaf scar.

5. CONCLUSIONS.

From what has been said, I think it is clear that the three species of *Lepidodendron* with which I am concerned here are quite distinct. Great variations in the form, size, and shape of the leaf base may occur in all of them, but the characters of the leaf scars are more constant and constitute the chief but not the only important diagnostic data. The chief peculiarities of these three species may be contrasted as follows:—

Character.	<i>L. lycopodioides.</i>	<i>L. ophiurus.</i>	<i>L. loricaum.</i>
Leaf scar	angular slit.	rhomboidal.	rhomboidal.
Orientation of leaf scar ..	straight.	straight.	usually oblique.
Prints of leaf scar	invisible.	faint or rarely visible, or only a central print is seen.	always visible.
Leaf base	fusiform.	fusiform.	napiform (subimbri-cated) or fusiform.
Ornamentation of keel ..	present	absent or very feeble.	absent.
Lower angle of leaf base ..	————	very obtuse.	acute.

The three species agree in the relatively small size of their leaf bases as compared with many others (e. g., *L. aculeatum*, Sternb.), and in the absence of sub-parichnoid prints. There is, however, much variation to be found among them, especially in the degree of angularity of the upper extremity of the leaf base, whether both its terminations are straight or bent, the position of the leaf scar relative to the centre of the leaf base, and the prominence of the keel.

Further, in addition to defining these species more accurately, an attempt is here made to institute a pure synonymy of these plants, especially with a view to establishing the nature of ancient types in the light of modern specimens.

It is shown that *L. lanceolatum*, Lesq., is identical with *L. lycopodioides*, Sternberg, and that *L. simile*, Jongmans, is a confusion between that species and *L. ophiurus*.

EXPLANATION OF THE PLATES.

(All the specimens figured are in the Carboniferous Plant Collections, Sedgwick Museum, Cambridge, to which the numbers refer. The photographs are by Mr. W. Tams, Cambridge.)

PLATE 10.

LEPIDODENDRON LYCOPODIODES, Sternb. (Pl. 10. figs. 1-9 & Pl. 11. figs. 10-16.)

- Fig. 1. No. 3205. Middle Coal Measures. Bishopsbourne Boring, Kent. (Nat. size.)
 Fig. 2. No. 3205. Middle Coal Measures. Bishopsbourne Boring, Kent. ($\times 2$)
 Fig. 3. No. 2754. Bond's Main Colliery, Temple Normanton, Derbyshire. (Nat. size.)
 Fig. 4. No. 107. Coal Measures. Toronley Colliery. Locality unknown. (Nat. size.)
 Fig. 5. No. 107. Coal Measures. Toronley Colliery. Locality unknown. ($\times 3$)
 Fig. 6. No. 927. Middle Coal Measures. Cannel Band, Flimby, Cumberland. (Nat. size.)
 Fig. 7. No. 927. Middle Coal Measures. Cannel Band, Flimby, Cumberland. ($\times 2$)
 Fig. 8. No. 950. Middle Coal Measures. Robin Hood Pit, Flimby, Cumberland. ($\times 3$)
 Fig. 9. No. 68. Coal Measures. Barnsley. ($\times 3$)

PLATE 11.

- Fig. 10. No. 103. Coal Measures. Jarrow. ($\times 3$)
 Fig. 11. No. 3475. New Mine Coal. Bentley, South Staffordshire. ($\times 1\frac{1}{2}$)
 Fig. 12. No. 754. Coal Measures. Bradford. (Nat. size.)
 Fig. 13. No. 755. Wax cast of specimen from Coal Measures. Bradford. (Nat. size.)
 Fig. 14. No. 3568. Wax cast of specimen, Claycroft, Cosely, South Staffordshire. ($\times 2$)
 Fig. 15 A. No. 3249. Between Bottom and New Mine Coal. Pouk Hill, Walsall. (Nat. size.)
 Fig. 15 B. No. 3249. Between Bottom and New Mine Coal. Pouk Hill, Walsall. ($\times 3$)
 Fig. 16. No. 1475. Near base of Lower Coal Measures. Queen's Seam, Broomhill Colliery, nr. Amble, Northumberland. (Nat. size.)

LEPIDODENDRON LANCEOLATUM, Lesq. = *L. lycopodioides*, Sternb.
 (Pl. 11. fig. 17 & Pl. 12. figs. 18-22.)

- Fig. 17. No. 1024. Coal Measures. 2nd Division. Lightmoor Colliery, Forest of Dean, Gloucestershire. (Nat. size.)

PLATE 12.

- Fig. 18. No. 1624. Coal Measures. 2nd Division, Lightmoor Colliery, Forest of Dean, Gloucestershire. ($\times 3$)
 Fig. 19. No. 1986. Coal Measures, 2nd Division, Park End Colliery, Forest of Dean, Gloucestershire. ($\times 3$)
 Fig. 20. No. 2507. Transition Coal Measures. Bayton Colliery, Forest of Wyre. ($\times 3$)
 Fig. 21. No. 2066. Upper Coal Measures. Shortwood Colliery, nr. Bristol. (Nat. size.)
 Fig. 22. No. 1625. 2nd Division, Lightmoor Colliery, Forest of Dean, Gloucestershire. ($\times 3$)

LEPIDODENDRON OPHIURUS (Brongn.). (Figs. 23-26.)

- Fig. 23. No. 131. Coal Measures. Locality unknown. (Nat. size.)
 Fig. 24. No. 131. Coal Measures. Locality unknown. ($\times 2$)
 Fig. 25. No. 3472. Coal Measures. Shallow Seam, West Cannock Colliery. No. 1 Pit, Hednesford, South Staffs. ($\times 3$)
 Fig. 26. No. 3478. Thick Coal. Cakemoor Colliery, Blackheath, South Staffs. ($\times 3$)



1.

5 (x3).



2 (x2).



W. Tams photo.



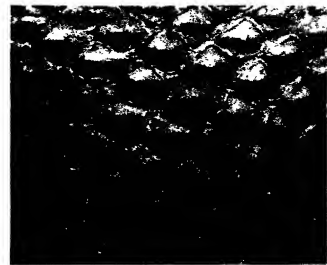
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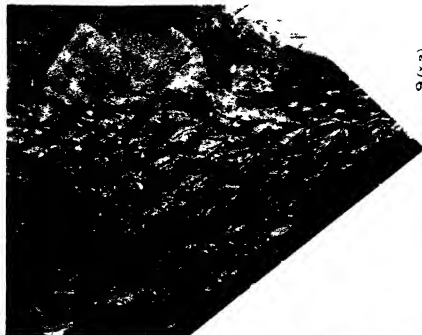
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6.



7 (x2).

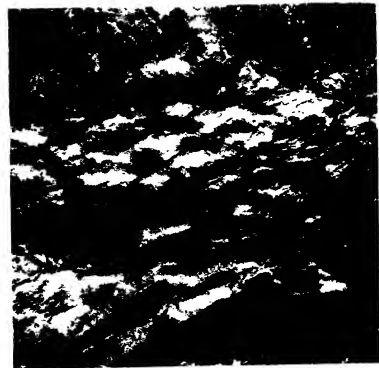


9 (x3)

8 (x3).

LEPIDODENDRON LYCOPODIODES, Sternb.

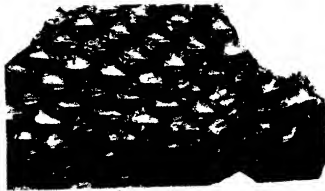
Huth coll.



10 (x3).



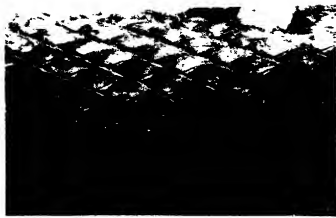
14 (x2).



12.



13.



17.



15^A (x3).



15^B



11 (x194).



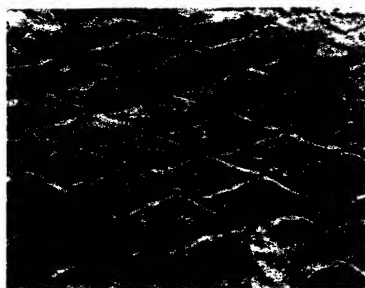
16.



18 (x8)



19 (x8)



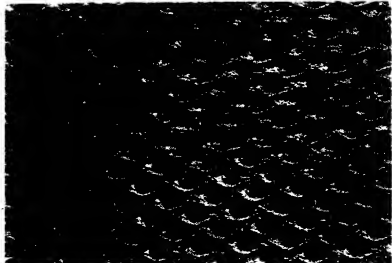
20 (x8)



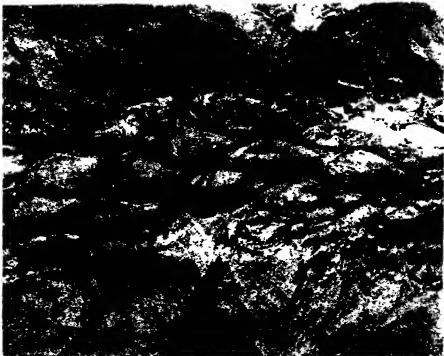
21.



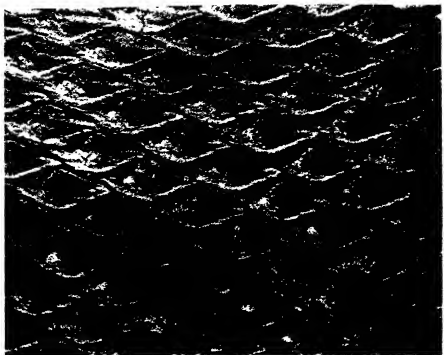
25 (x8)



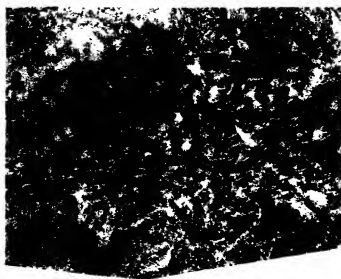
23.



22 (x8)



24 (x8)

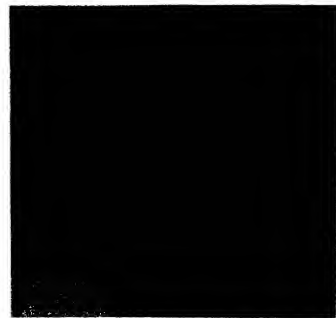


26 (x8)

LEPIDODENDRON LANCEOLATUM, Lesq. - L. LYCOPODIODES, Sternb. Figs. 18-22. L. OPHIURUS, Brongn. Figs. 23-26.



27.



28 (x2).



29 (x3).



34 (x2).



35 (x3).



33.



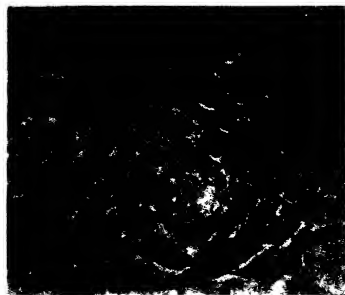
36.



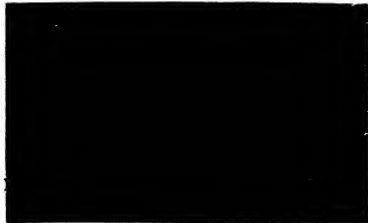
32 (x3).



31.



30 (x2).



37 (x3)

Huth coll.

LEPIDODENDRON LORICATUM, sp. nova.

PLATE 13.

LEPIDODENDRON LORICATUM, sp. nova. (Figs. 27-37.)

- Fig. 27. No. 2506. Transition Coal Measures. Bayton Colliery, Forest of Dean. (Nat. size.)
 Fig. 28. No. 2506. Transition Coal Measures. Bayton Colliery, Forest of Dean. ($\times 2$)
 Fig. 29. No. 2470. Transition Coal Measures. Barfreston Boring, Kent. ($\times 3$)
 Fig. 30. No. 959. Ardwick Series. Manchester. ($\times 2$)
 Fig. 31. No. 3109. Transition Coal Measures. Chilton Boring, Kent. (Nat. size.)
 Fig. 32. No. 3109. Transition Coal Measures. Chilton Boring, Kent. ($\times 3$)
 Fig. 33. No. 1645. Upper Coal Measures. Flour Mill Colliery, Forest of Dean, Gloucestershire. (Nat. size.)
 Fig. 34. No. 1645. Upper Coal Measures. Flour Mill Colliery, Forest of Dean, Gloucestershire. ($\times 2$)
 Fig. 35. No. 1953. Coal Measures. Trafalgar Colliery, 2nd Division, Forest of Dean, Gloucestershire. (\times nearly 3.)
 Fig. 36. No. 3130. Transition Coal Measures. Chilton Boring, Kent. (Nat. size.)
 Fig. 37. No. 3130. Transition Coal Measures. Chilton Boring, Kent. ($\times 3$)

III. NEUROPTERIS OBLIQUA, Brongn., and N. CALLOSA, Lesq.

1. INTRODUCTION.

It appears to me that some confusion has arisen between the frond species known as *Neuropteris obliqua*, Brongn., *Neuropteris acuminata*, Zeiller, and *Neuropteris impar*, Potoulié. At any rate, it will be admitted that considerable differences of opinion have existed as to whether some or all of these forms are or are not identical, and as to the principal characters by which they may be distinguished from one another and from other species. I give here the results of my re-examination of these questions. The difficulty appears to arise from the dimorphic nature of a species here termed *N. obliqua*, Brongn., and also from a confusion which has arisen between one form of this species and a plant which I find to be entirely distinct, and which I believe to be the *Neuropteris callosa* of Lesquereux.

I begin with a consideration of the former species.

2. NEUROPTERIS OBLIQUA (Brongn.).

Synonymy of *Neuropteris obliqua*, Brongn. :—

A. Minor Pinnules.

1832. *Pacopteris obliqua*, Brongniart, Hist. Vég. Foss. p. 320, pl. 96. figs. 1-4.
 1880. *Odontopteris binervosa*, Achebuhl, Niederrhein.-Westfäl. Steinkohlengebirge, Oberhausen und Leipzig, p. 118, pl. 36. fig. 5.
 1903. *Neuropteris obliqua*, Arber, Quart. Journ. Geol. Soc. vol. lix. p. 4, pl. 1. fig. 2.
 1907. ? *Mixoneura obliqua*, Zalesky, Bull. Com. Géol. St. Pétersbourg, vol. xxvi. No. 134 p. 404, pl. 15. figs. 11, 12, & 16.
 1907. *Mixoneura obliqua*, Zalesky, *ibid.* No. 135, p. 479, pl. 19. figs. 1, 3-9.
 1913. ? *Neuropteris obliqua*, Gothan, Abhandl. k.-preuss. geol. Landesanst. N.F. Heft 75, p. 207, ? pl. 50. fig. 5, pl. 53. fig. 5.

B. Major Pinnules.

- 1886-88. *Neuropteris acuminata*, Zeiller, Flore Foss. Bass. Houill. Valenciennes, p. 255, pl. 41. fig. 4.
 1906. *Neurodontopteris obliqua*, Gothan, in Potonié, Abbild. und Beschr. Foss. Pflanzen, Lief. iv. No. 68, text-figs. 2B, 4, 5, pl. unnumbered, following p. 11, fig. B.
 1907. *Mixoneura obliqua*, Zalessky, Bull. Com. Géol. St. Pétersbourg, vol. xxvi. No. 134, p. 479, pl. 19. figs. 2 & 10.
 1910. *Neuropteris acuminata*, Arber, Proc. Yorks. Geol. Soc. vol. xvii. pt. ii. p. 138, pl. 17. fig. 3.
 1911. *Neuropteris impar*, Kidston, Mém. Mus. R. Hist. Nat. Belgique, vol. iv. p. 83, pl. 8. figs. 2, 3, 3a.

C. Major and Minor Pinnules.

1837. ? *Neuropteris heterophylla*, Lindley & Hutton, Foss. Flora, vol. iii. p. 90, pl. 183.
 1893. *Neurodontopteris impar*, Potonié, Jahrb. k.-preuss. geol. Landesanstalt für 1892, p. 1, pl. 1. figs. 1, 2, 4.
 1906. *Neurodontopteris obliqua*, Gothan, in Potonié, Abbild. und Beschr. Foss. Pflanzenr. Lief. iv. No. 68, pl. unnumbered following p. 11, fig. B.
 1911. *Neuropteris impar*, Kidston, Mém. Mus. R. Hist. Nat. Belgique, vol. iv. p. 83, pl. 8. fig. 1.

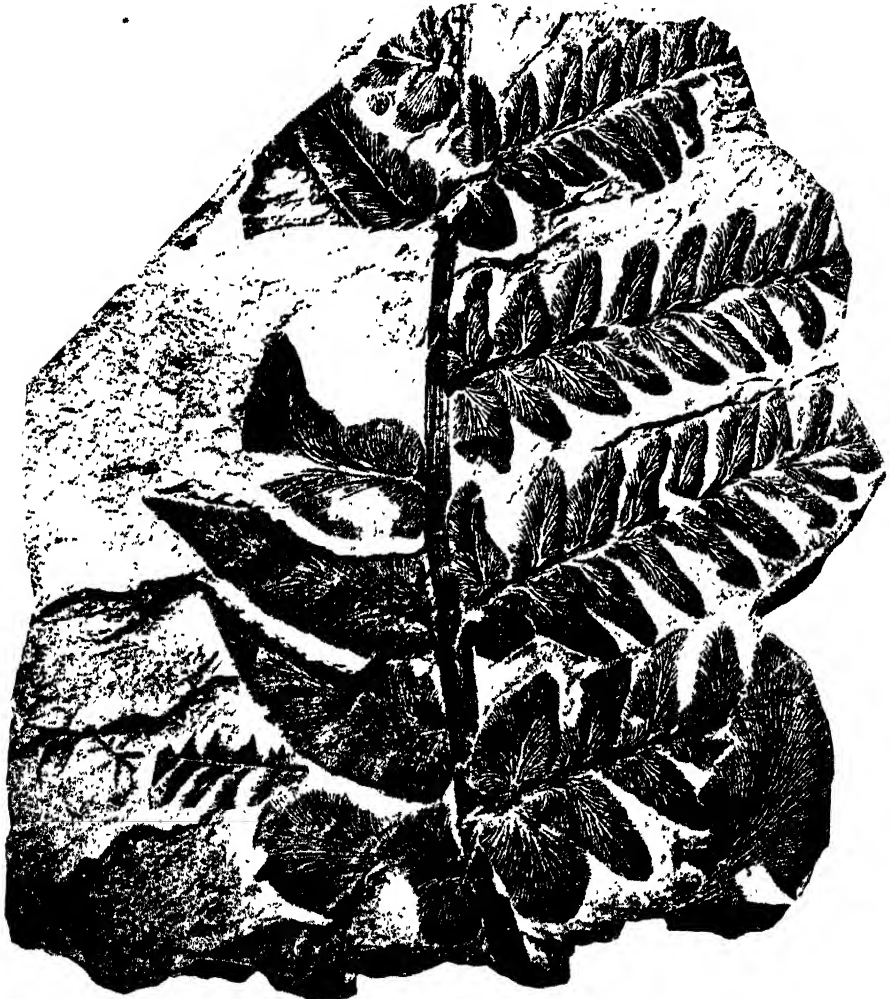
Remarks on the Synonymy of Neuropteris obliqua, Brongn.

Neuropteris obliqua (Brongn.) is a species of Coal-measure frond which has already caused considerable trouble and confusion. We are as yet probably not at an end of our difficulties in this respect. These fronds were, like those of certain other species of the genus, dimorphic. On one side of the frond we may find pinnæ composed of a large number of small triangular pinnules here termed minor pinnules, while, on the other, simple, large, ovate-lanceolate leaflets may occur, here called the major pinnules. Or, again, the pinnæ may consist solely of major or minor pinnules. The minor pinnules, which were the first described portions of these fronds, are often typically Odontopteroid. They are often decurrent, and, further, a considerable portion of the lateral nerves arise directly from the rachis and not from the median nerve, which is weak. They are very little arched, but are sinuous in their course, each nerve dichotomising two or three times. The sinuous course of the nerves necessitates unequal intervals of lamina between the nerves, and this feature is highly characteristic of this species.

Did the evidence end here, this species would be more correctly classed with *Odontopteris* than *Neuropteris*, especially on account of the attachment of the pinnules and the origin of the lower lateral nerves. It has, in fact, been placed in that genus by more than one authority, while Potonié expressed the facts by suggesting a new genus *Neurodontopteris*, which, however, has not been adopted by other workers. Similar resemblances occur to other genera, such as *Alethopteris* and *Callipteris*. In fact, the definitions of these form-genera break down over such cases as this, and it is purely a matter of convention in which genus this species is placed.

The major pinnules were first known in 1886, and were regarded as a separate species. Neglecting two early figures, about which considerable doubt exists [the *Neuropteris heterophylla* of Lindley and Hutton (20. iii. pl. 183), the type of which is lost, but which may be a specimen of

FIG. 1.



Neuropteris obliqua, Brongn. Major and minor pinnules. Potonié, H., Ueber einige Carbonfarne, IV. Theil, 1893, pl. 1. fig. 1. *Neurodontopteris impar* (Weiss) Potonié.

N. obliqua incorrectly drawn, and also the *Neuropteris Scheuchzeri* of SauvEUR (24. pl. 34. fig. 2)], we have the specimen figured by Zeiller in 1886 (27. p. 255, pl. 41. fig. 4) as *N. acuminata*. In this specimen the pinna is composed entirely of the major pinnules. Other excellent examples of these pinnules have been

more recently figured by Kidston (15. p. 83, pl. 8. figs. 2, 3, 3a). The major pinnules are large, very variable in shape, and the leaflets resemble those of *Neuropteris Scheuchzeri*, Hoffm., somewhat in habit. They are not attached by the whole base, but by a restricted portion, which is, however, sufficiently broad sometimes to allow of the origin of some of the lateral basal veins directly from the rachis. The lateral nerves are more frequently dichotomised than in the minor pinnules, but possess a similar inclination, and are also sinuous in their course.

The continuity between the minor pinnules (*N. obliqua* of Brongniart) and the major (*N. acuminata* of Zeiller) was first proved in a specimen discovered by Weiss, but described by Potonié in 1893 as *Neurodontopteris impar*. This frond shows simple major pinnules on one side and pinnate pinnæ composed of minor pinnules on the other (fig. 1, p. 209).

Potonié (22) does not appear to have recognised the identity between the minor pinnules of this specimen and the *Neuropteris obliqua* of Brongniart, and even Kidston (15) expresses himself as not quite convinced on this point, though he regards it as highly probable. Gothan (11. p. 207), however, has more recently referred these specimens to Brongniart's species, and with this conclusion I am also in agreement. It is thus clear that the terms *N. acuminata*, Zeill., and *N. impar*, Pot., are mere synonyms of *N. obliqua*, Brongn.

Neuropteris obliqua was known to me chiefly by the major pinnules—of which there is a good collection from several coalfields in the Sedgwick Museum, Cambridge—until a few years ago, when I collected undoubted examples of the minor pinnules from the Middle Coal Measures of Bond's Main Colliery in Derbyshire. It is true that I had imagined that one already possessed at Cambridge many specimens of these minor pinnules, but as soon as I had acquired the Derbyshire specimens I realised that I—and, as I believe, others also—had been confusing a quite distinct, though similar, plant with the true *Neuropteris obliqua*. This other type of frond, which is much more abundant in Britain than *N. obliqua*, is here redescribed under the name *N. callosa*, Lesq.

Remarks on Specimens here figured.

Excellent illustrations of this species have already been published, so only a few selected types are figured here for comparison with the distinct species *N. callosa*, Lesq.

No. 1430. On Pl. 14. fig. 1 is seen, natural size, a typical pinna bearing major pinnules of the lanceolate type below and passing above into minor pinnules. The larger pinnules have a distinctly sinuate margin. The nervation is very clear, except at the base of the pinnules.

No. 2180. Another specimen from the Ingleton Coal Measures is also

figured, natural size, on Pl. 14. fig. 2. Here the lanceolate pinnules are seen partly dissected at the base into minor pinnules, a transition from the major to the minor type of pinnule. The apical portions are broadly lanceolate.

No. 1362. An example from the Middle Coal Measures of Barnsley, Yorkshire, with very large major pinnules of the ovate-lanceolate type, is figured on Pl. 14. fig. 3, natural size. These pinnules measure 5 cm. in length by 2.5 cm. in breadth.

No. 1708. An example of part of a pinna with minor pinnules is shown, natural size, on Pl. 14. fig. 4, and enlarged in fig. 5 to emphasize the nervation. The pinnules are here elongately oval, 2 cm. in length by nearly 1 cm. in breadth. They are attached by a considerable portion of the base. A few of the basal nerves, in addition to the median nerve, arise directly from the rachis. The sinuous course of the subdivisions of the median nerve and their spacing in the centre of the leaflet are characteristic.

No. 2793. Typical pinnules of the minor type are seen, natural size, on Pl. 14. fig. 6 (left-hand side), and enlarged twice in fig. 7 (left-hand side). This specimen is from the Middle Coal Measures of Bond's Main, Derbyshire.

The pinnules vary slightly in shape, but are elongately oval, 8 mm. or less in length and 3.5 mm. or less across. They are attached by their whole base, somewhat decurrent, and a large part of the lower nervation arises directly from the rachis. The terminal pinnule is elongate and narrow.

No. 2798. The nervation in a similar case from the same locality is also seen enlarged on Pl. 14. fig. 8 A.

Diagnosis of Neuropteris obliqua, Brongn.

Frond dimorphic, composed entirely of minor or of major pinnules, or containing pinnules of both types. Minor pinnules small, up to 2 cm. long and nearly 1 cm. broad, often considerably smaller, elongately oval or elongately triangular, more or less parallel-sided, attached to the axis by the whole base or, in the broader types, only by part of the base. Apical pinnule very large or long and narrow. Lateral nerves very clear, not very stout; a considerable portion of the lateral nerves arise directly from the rachis and not from the median nerve. Lateral nerves very little arched, sinuous, each dichotomising 2-3 times, markedly distant from one another in centre of leaf. Major pinnules very variable in size and shape, even in the same pinna, lanceolate (up to 2.5 x 1 cm.), ovate-lanceolate (up to 5 x 2.5 cm.), oval or semicyclopteroid (about 3.5 x 2.5 cm.), sometimes very broad and unsymmetrical, attached to the rachis by a very small part of the base, which, however, is sometimes sufficiently broad to allow of the origin of some of the basal lateral veins directly from the rachis. The lanceolate

pinnules are frequently lobed or divided into minor pinnules at the base. The cyclopteroid-like pinnules have a broader point of attachment and a more radiating nervation, partly arising directly from the rachis. The lateral nerves are more frequently dichotomised than in the minor pinnules, but possess a similar inclination and are also sinuous in their course.

Distribution.

The following is the distribution of this species in Great Britain, so far as it is known to me :—

Middle Coal Measures.

Derbyshire Coalfield :—Top Hard Coal, Shipley Clay Pit, Derby.

Yorkshire Coalfield :—Above Silkstone Coal, Bond's Main Colliery, Derbyshire. Old Hards Coal, Hartley Bank Pit, Horbury, Yorks. Horizon uncertain, Barnsley, Yorks.

Ingleton Coalfield :—W. of Ingleton.

Denbighshire Coalfield :—Llag Hill near Wrexham.

? Kent Coalfield.

Devonshire.

Lower Coal Measures.

Northumberland Coalfield :—Horizon uncertain, Felling.

3. *NEUROPTERIS CALLOSA*, Lesq.

I turn now to another type, which I hope to be able to show here is quite distinct from *N. obliqua*, Brongn., but which has been confused with it, although it is of very much commoner occurrence than that species. This plant I believe to be the *Neuropteris callosa* of Lesquereux, a species which has already been doubtfully recorded by Dr. Kidston from three British coalfields.

Synonymy of *Neuropteris callosa*, Lesquereux :—

1879-80. *Neuropteris callosa*, Lesquereux, 2nd Geol. Surv. Pennsylv. p. P. 115, pl. 16. figs. 1-4 (? figs. 5-8).

1909. *Neuropteris obliqua*, Arber, Quart. Journ. Geol. Soc. vol. lxx. p. 26, pl. 1. fig. 3.

1911. *Neuropteris obliqua*, Kidston & Jongmans, Arch. Néerl. Sci. Exact. et Nat. ser. 3 B, vol. i. p. 25, pl. (unnumbered), fig. 3.

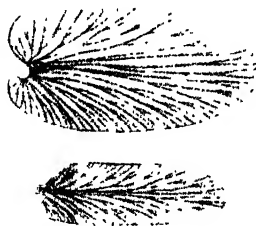
Remarks on the Specimens previously figured.

Lesquereux's type was diagnosed as follows :—"Bipinnate; ultimate pinnæ linear; leaflets alternate, sessile by a broad base, oblong or oval, obtuse; veins flabellate from the base, strongly marked, slightly curved; cyclopterid pinnules cordate at the point of attachment, unequilateral, polymorphous."

Of Lesquereux's figures, pl. 16. figures 2-4, are the most characteristic. Two of these figures are reproduced in text-fig. 2, p. 213. The bluntly

oblong-oval pinnules slightly eared at the base, the sinuate nerves, erect and little arched, dichotomising three times or less, are features all clearly portrayed in these figures. Cyclopteroid pinnules similar to those shown by Lesquereux on pl. 16. figs. 6 & 8, are often associated with this plant, but, so far as I am aware, they have not been found in continuity, and I therefore hesitate to apply the specific name to them.

FIG. 2.



Neuropteris callosa, Lesq. Pinnules to show nervation. Lesquereux, L.
Atlas to the Coal Flora of Pennsylvania, 1879, pl. 16.

The specimen from Kent figured by myself in 1909 and the seed-bearing examples described by Kidston and Jongmans in 1911, both referred to *N. obliqua*, now appear to me to be identical with Lesquereux's plant.

So far as I am aware, these are the only trustworthy examples of this very common type which have yet been figured, though, among the many hundreds of Neuropterids described on the Continent, there may, of course, be some which on re-investigation would prove to be identical.

Description of the Specimens figured here.

No. 2730. Part of the pinna of this species is shown natural size on Pl. 15. fig. 9, and some pinnules from the same specimen in fig. 10. enlarged three times to show the nervation.

The pinnules in this case are rather small, the largest being about 7 mm. or less in length and 5 mm. across at their widest point. They are strictly oval. The terminal pinnule is narrow and rather short in this case, though in some instances here its full length is not disclosed. The pinnules are closely set on the rachis and sometimes overlap one another slightly. They are very slightly eared at the base. The nerves (fig. 10) are clear, but fine and nearly all of equal strength. They are slightly arched and flexuous and equally spaced.

No. 613. Pinnules from another specimen are shown nat. size in Pl. 15. fig. 11 A, and enlarged ($\times 2$) in fig. 11 B. The pinnules here are larger, some of them being about 1 cm. long.

No. 1170. Some pinnules, larger still, are shown magnified three times in fig. 12. Some of these measure 12 mm. in length. The characteristic nervation is clearly seen.

No. 2381. The terminal region of the pinna in which some of the pinnules reach a length of 15 mm. is shown enlarged twice in fig. 13. The tip of the terminal pinnule is hidden in the rock.

No. 2632. A fragment of an apical portion of a pinna in which the pinnules are very small, but the nerves clearly seen, is shown in fig. 14, enlarged three times.

No. 1916. In fig. 15 an enlarged photograph of a specimen from the Kent coalfield, which I figured in 1909, is given. The pinnules are here elongately oval, nearly 2 cm. long, and overlap one another.

Diagnosis of Neuropteris callosa, Lesq.

Frond large, tri- or ?quadripinnate. Penultimate pinnæ broad, often but not always with a broad axis; ultimate pinnæ lanceolate, axis very slender. Pinnules typically Neuropteroid, inserted by a very small part of the base, oval or elongately oval, varying much in size from about 4 mm. up to 20 mm. or more in length, entire, broadly rounded at the apex, markedly cordate, almost eared at the base, closely set on the axis, and frequently overlapping one another. Pinnules markedly caducous. Nervation clearly marked, but nerves fine, all nearly equally strong and equally spaced, lateral nerves all arising from the median nerve, not crowded, somewhat arched, flexuous in their course, dichotomising once to three times. Lamina between the veins frequently punctate. Terminal pinnule rather small, elongately lanceolate or oval-lanceolate.

Distribution.

The distribution of *Neuropteris callosa*, Lesq., in this country, so far as it is known to me, is:—

Transition Coal Measures.

Kent: Several borings at Waldershare, etc.

Middle Coal Measures.

Kent: Many borings at Goodnestone, etc.

Pembrokeshire: Rickets Head, near Newgate, etc.

Wyre Forest: Kinlet, Alton Boring, No. 1.

Titterstone Clee Hills: South Coal.

Yorkshire (Derbyshire): Below Top Hard Coal, Shipley.

Yorkshire: Monkton Main Colliery.

? Ingleton: Ingleton Colliery.

Doubtful records which I have not seen are:—

Transition Coal Measures.

? South Lancashire: Bradford Colliery, Manchester [Gerrard (10. p. 561) & Kidston (17. p. 321)].

Middle Coal Measures.

? Leicestershire Coalfields:—Bretby, S. Derby (Horwood, 13. p. 154).

4. CONCLUSIONS.

From the specimens figured here I think it will be clear that *Neuropteris callosa*, Lesq., is quite distinct from *N. obliqua*, Brongn. The pinnules of the former could only be mistaken for the minor pinnules of the latter. In both cases the nerves are slightly flexuous, but the insertion of the pinnules, the origin of the basal nerves, and the spacing of the veins in the latter species will alone serve to distinguish this type from *N. callosa*. On the other hand, *N. callosa* lies much nearer to other species of the same genus, especially *N. tenuifolia* (Schl.), and, in a more remote degree, *N. heterophylla*, Brongn. In *N. tenuifolia*, however, the pinnules are usually much larger, the veins are not flexuous, the median nerve is much stronger near the base of the pinnule, and the lateral nerves are often more distinctly arched and highly divided. *Neuropteris callosa* is distinguished from *N. heterophylla* by the fact that the pinnules do not become decompound as in that species. The nervation in *N. heterophylla* is also much coarser and more crowded, and the veins are not flexuous, but more frequently dichotomised.

At the same time it must be admitted that difficulties in discriminating between all these species may arise when dealing with fragmentary or not exceptionally clear materials, or with certain portions of pinnae. I am, for instance, still rather in doubt as to which species the specimens figured by Zeiller in his Valenciennes Flora (page 48) under the name *N. obliqua* belong to, though I am inclined to think they are there correctly named and are distinct from *N. callosa*, Lesq.

EXPLANATION OF THE PLATES.

All the figures are from photographs by Mr. W. Tams, of Cambridge, from specimens in the Sedgwick Museum, Cambridge. The numbers refer to the Carboniferous Plant Collections in that Museum.

PLATE 14.

NEUROPTERIS OBLIQUA, Brongn. (Figs. 1-8.)

Fig. 1. Coal Measures, locality unknown, No. 1430 (nat. size).

Fig. 2. " " Ingleton Colliery, No. 2180 (nat. size).

Fig. 3. " " Barnsley, No. 1362 (nat. size).

Figs. 4 & 5. " " locality unknown, No. 1708. Fig. 4 (nat. size). 5 ($\times 3$).

Figs. 6 & 7. Above Silkstone Coal, Bond's Main Colliery, Temple Normanton, Derby, No. 2793. Fig. 6 (nat. size). Fig. 7 ($\times 2$).

Figs. 8 A & 8 B. Above Silkstone Coal, Bond's Main Colliery, Temple Normanton, Derby, No. 2798 ($\times 2$).

PLATE 15.

NEUROPTERIS CALLOSA, Lesq. (Figs. 9-15.)

Figs. 9 & 10. Coal Measures, Sheffield, No. 2730. Fig. 9 (nat. size). Fig. 10 ($\times 3$).

Figs. 11 A & 11 B. Coal Measures, locality unknown, No. 613. Fig. 11 A (nat. size). Fig. 11 B ($\times 2$).

Fig. 12. Coal Measures, Wakefield or Pontefract, No. 1170. ($\times 3$).

Fig. 13. Middle Coal Measures, Matfice Hill, Sandwich, No. 2381. ($\times 2$).

Fig. 14. Sweet Coals, Kinlet Colliery, Wyre Forest, Salop, No. 2632. ($\times 3$).

Fig. 15. Transition Coal Measures, Waldershare Boring, Kent, No. 1916. ($\times 2$).

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1.



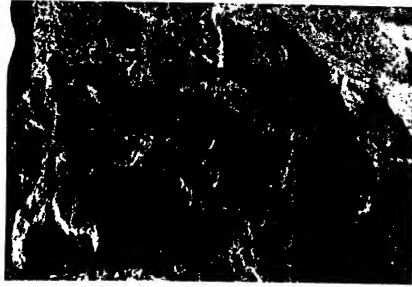
2.



4.



3.



8^a (x2).



5 (x8)



6.

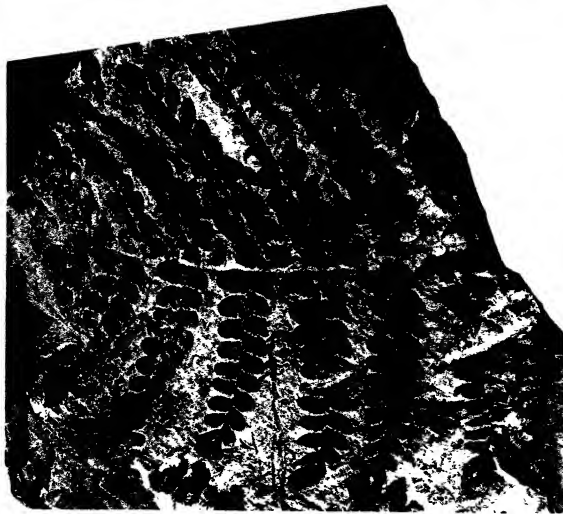


7 (x2)



8^a (x2)
Hubb coll

NEUROPTERIS OBLIQUA, Brongn.



10 (x9).



11A

W Tama photo.



12 (x2).



12 (x9)



11B (x2).



14 (x9).



15 (x2)

Hutch coll

NEUROPTERIS CALLOSA, Lesq.

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HOOKER LECTURE.

A STUDY IN CONTRASTS :

The Present and Past Distribution of certain Ferns.

(With PLATES 16-19.)

THURSDAY, 1st JUNE, 1922.

BY A. C. SEWARD, Sc.D., F.R.S., F.L.S., PRES.G.S.

A BOTANIST, especially one whose interest is not limited by the world of to-day, feels a certain kinship with the Archaeologist who seeks information on the life and nature of the people who fashioned and used the materials discovered in the course of excavations. "For the Vegetable kingdom also," as Asa Gray said, "there is a veritable archaeology." In Central Asia Sir Aurel Stein traced for a considerable distance the foundations of a wall constructed in the second century B.C., and among the litter of the guard-rooms by the gates found fragments of letters, orders of the day, and other records which enabled experts not merely to reconstruct the wall, but to see the guards at their daily tasks and even to look into their minds. The discovery of a deposit rich in fossil plants throws light on some points interesting to the systematist or to the student of plant geography ; but our aim is more than this—it is to see in imagination the plants of other days as though they still lived, and, if data are available, to set in motion the mechanism of the organism and reproduce something at least of the conditions under which it grew.

The impression made upon the mind by the first glimpse of some feature in the landscape rendered classic by historical or mythical association finds expression in a desire to give rein to the fancy ; the object seen, whether mountain, hill, or valley, is transported to dreamland and peopled by a vanished race. I would not go so far as to suggest that every man of science should take as his guide Sir Thomas Browne's dictum "where I cannot satisfy my reason, I love to humor my fancy" ; but there is gain rather than loss even in the treatment of scientific facts if some play, tempered by a becoming sense of proportion, is allowed to the imagination.

My object to-day is to give a few examples of the application of palæobotanical enquiry to problems of plant geography ; to endeavour to follow for a short distance into the ages which man never knew the history of some families of Ferns ; to trace their wanderings and if possible to discover their original homes. The alluring task of interpreting and reconstructing the relics of ancient floras has its dangers and limitations : our efforts to make them live may produce a state of mind like that of a College Biographer who describes how in a nightmare he heard from an assembly of past generations of men whose lives and deeds he had attempted to portray, a hum of deep dissatisfaction directed against some one who they declared had scandalously misdescribed their careers in life.

No apology is needed from anyone honoured by an invitation to deliver the Hooker Lecture who chooses as his subject a problem connected with geographical distribution ; it is the quality of the matter and not the theme which causes misgiving. The study of plant geography if confined to the present must obviously be incomplete ; the data gathered from existing plants must be supplemented by records of the rocks—records, as Darwin said, which represent a short chapter of the last volume of a history imperfectly kept, and of this chapter only here and there a few lines. Though in all palæobotanical work the student is necessarily at a disadvantage because of the poverty of the documents, there are certain groups and families which promise some measure of success. The remarkable series of papers by Prof. Bower on several recent Ferns, which forms a worthy continuation and extension of the work of the Hookers, has stimulated botanists to take a wider interest in the inter-relations and past history of the several families.

Once established, Ferns have a considerable power of spreading by vegetative means ; the lightness and resistant nature of the spores enable them to play a successful rôle as colonisers and as emigrants to new countries. When Treub visited the remnant of the devastated Island of Krakatau three years after the series of violent eruptions he found eleven species of Ferns among the pioneers of the new flora. As a class Ferns are cosmopolitan, though certain families, genera, and species are strictly limited in range and highly sensitive to the influence of physical or climatic conditions. The familiar Bracken Fern illustrates in a wonderful degree capacity for adaptation to different climates and success as a traveller ; but in what part of the world its journey began we cannot tell. Far within the Arctic circle *Cystopteris fragilis* lives through the Greenland winter ; it grows in Morocco, Abyssinia, and South Africa and extends along the Andes through several degrees of latitude. *Polystichum Lonchitis* is at home at an altitude of 2000 metres in the Swiss Alps ; it flourishes in Northern Greenland, North America, Northern India, and in China. Another species, *Polystichum capense*, occurs in the Island of New Amsterdam in lat. 37° 5' S., where it is said to grow almost as high as a man, and on the high plateau of Juan

Fernandez. The latter island is also the home of *Thyrsopteris elegans*, a Fern which occurs nowhere else in the world: is this species a new creation which has not had time to spread, or is it the last of a long line of ancestors which in a former period of the earth's history occupied a much more extended territory? *Thyrsopteris* is very closely allied to certain Jurassic Ferns from the Yorkshire coast and many other places: geological evidence points to a remote antiquity, and its present isolation is in all probability the last phase in the history of a direct derivative of a widely scattered Jurassic type.

Though by no means unrepresented in desert regions, Ferns are in the main mesotherm hygrophytes: several families include markedly xerophilous representatives, and even the Maidenhair Fern, *Adiantum Capillus-Veneris*, grows in sheltered and moist places in the arid regions of Mesopotamia and Central Asia. It is in the moist atmosphere of tropical and sub-tropical islands that Ferns reach their richest development. It has been stated that Ferns are particularly sensitive to climate and therefore valuable as climatic indicators. While admitting that existing Ferns are as a whole associated with certain types of habitat, the capacity exhibited by several species for enduring strongly contrasted conditions detracts from their value in enquiries into the climates of the past.

Dr. Willis, whose contributions to the subject of geographical distribution have deservedly attracted much attention, admits that there are exceptions to his general law of Age and Area which classes species and genera of restricted range among the more recent products of evolution; but thoroughly to appreciate the inward meaning of distribution, regard must be had to past history. Intimately connected with enquiries based on phytogeographical data are questions of inter-relationships of genera and families. The researches of Prof. Bower enable us to acquire a clearer conception of the natural classification of Ferns. He believes that "the most positive line we possess in the broad avenue of botanical phylogeny is that of palæophytology." Without a strict application of what he happily calls the palæontological check we cannot interpret phytogeographical facts with much hope of satisfactory results, nor can we with any confidence assign existing families to their respective positions in an evolutionary sequence. In the words of a seventeenth century divine, "without history a man's soul is purblind, seeing only the things which almost touch his eyes."

My aim is to connect as clearly as may be the Past with the Present without over-emphasising the boundary between what is and what was. If we confine ourselves to the Present the plant world appears to be in an almost static condition: viewed by itself it produces no impression of change on a large scale; but imagination has fuller scope when among the relics of a bygone vegetation we discover strange types that stimulate our fancy, and evolution becomes a relatively rapid process. The linking up into series of

forms from different geological periods tends to reduce to a minimum the idea of time and gives a false impression of rapid change.

“ Thus ignorant of man and of the ages
That he calls ancient, ignorant of all
The sons who follow as their grandsires led,
Stands Nature ever young—
Or rather she *proceeds*, but so long
A course she seems to *stand*.”

I propose to pass in review the following families:—the Gleicheniaceæ, the Matonineæ, the Dipteridina, the Schizæaceæ, the Marattiaceæ. It must be frankly acknowledged that I am travelling over a familiar road; my object is rather to bring together some of the facts already published both by other palæobotanists and by myself than to attempt to add much that is new. Palæozoic forms are excluded partly because of the difficulty of precise statement on their affinity, but chiefly because it is not until the Mesozoic era that existing types become clearly defined. Before dealing with these families brief reference will be made to the genus *Onoclea*, a member of the Polypodiaceæ which is probably the most modern though by far the richest in genera of all fern families.

*Onoclea sensibilis**, the only species of *Onoclea* recognised by some authors, is characterised by dimorphic fronds, the sterile leaves having linear pinnæ entire or lobed and with anastomosing veins, the fertile leaves bearing pinnate branches almost devoid of laminae with small infolded lobes enclosing sori. This Fern ranges from Florida to Newfoundland and to Nebraska in the west; it occurs also in the far east of Asia. Fossil leaves, some of them indistinguishable from those of the recent plant, are recorded from Upper Cretaceous rocks in Colorado, Dakota, Montana, and in other parts of the United States; precisely similar specimens occur in Lower Tertiary strata in Western Greenland and in the Island of Mull. The recent discovery of well-preserved spores by Mr. Edwards of the British Museum on some of the Mull material confirms the identification of the sterile and fertile fronds. A well-known paper by Asa Gray first demonstrated the resemblance between the existing vegetation of the Eastern region of North America and that of Japan, a resemblance which it is generally believed extended to Europe in pre-Glacial times. Hooker in his classic paper on Arctic floras accepts Darwin's hypothesis, based on opinions first advanced by Edward Forbes, that from circumpolar land plants migrated to the South along divergent lines as the oncoming Glacial period caused a lowering of temperature. The work of Mr. and Mrs. Clement Reid on the later Tertiary floras of Western Europe has afforded striking testimony of the

* Photographs of recent and fossil Ferns were shown on the screen in illustration of the lecture,

correctness of this general principle: migrants to America and the Far East still survive, while many of those which followed a more direct southerly route perished by the way or were unable to reach the warmer regions in the South. At first sight the past distribution of *Onoclea* would seem to fall into line with the wanderings of later Tertiary plants; but if the American fossil *Onocleas* are correctly referred to an Upper Cretaceous horizon, while those from Greenland and Mull are Tertiary in age, some other interpretation must be sought. It is important, therefore, to review the evidence more fully than is possible in this lecture, and to enquire further into the relative age of the beds in which *Onoclea* has been discovered.

GLEICHENIACEÆ.

Though in the main the nomenclature of Christensen's invaluable 'Index Filicum' is followed, an exception is made in assigning generic rank to the tropical Australian Fern, *Platyzoma microphylla*, which the Danish author regards as a subgenus of *Gleichenia*: this departure from authority is, I venture to think, justified by the recent work of Prof. Thompson, of Liverpool. The genus *Gleichenia* includes two subgenera, *Eugleichenia* and *Dicranopteris*: the latter designation is, however, used by Underwood in place of the more familiar *Mertensia* as a title of generic rank equivalent to *Gleichenia*. *Gleichenia* in the wider sense includes over 100 species, the great majority of which are characterised by the possession of dichotomously branched fronds endowed with a power of unlimited growth. Though Goebel objects to the common practice of describing *Gleichenia* fronds as dichotomous, it is generally agreed that the method of branching is a form of dichotomy, and, as Dr. Boodle has suggested, the pinnate habit of the great majority of Ferns is probably a derivative of a more primitive dichotomous system. There are few Ferns which it is easy to recognise by frond habit alone. The West Indian Bramble Fern (*Odontosoria aculeata*) has dichotomously branched fronds, but the pinnules are entirely different from those of *Gleichenia*. With the exception of *Matonia pectinata* and *M. Foxworthyi* there are no recent Ferns which, without reference to soral characters, could be mistaken for *Gleichenia*. The strong rachis with its periods of rapid elongation and inactivity may reach a height of over 20 feet, giving off in regular stories forked pinnæ bearing linear segments usually 3 to 4 cm. long, but in rare cases as long as 10 cm. and more. As Underwood says, herbarium specimens give a very inadequate idea of the habit and size of the splendid fronds of this genus. The linear form of segment with the sori either in the middle or in the fork of the lateral veins is one of the distinguishing features of the subgenus *Dicranopteris*. In *Eugleichenia* the segments are for the most part semicircular, 2 to 3 mm. broad, and the sori are borne on the ends of lateral veins. The minute segments of some species look like small crenulations on the axes of the pinnæ, and when the

lamina is strongly revolute the rolled segments resemble a miniature billet moulding, e. g. in *G. dicarpa* and *G. alpina*. The bud or partially unrolled crozier in the fork of a *Gleichenia* rachis is often accompanied by modified pinnules which serve a protective function: these are sometimes described as *Aphlebiæ*, a designation criticised by Goebel on the ground that they are merely special forms of pinnules. The *Aphlebiæ* may have the shape of ordinary segments, but they are occasionally larger and broader and may be bipinnate. In some species, e. g. *Gleichenia linearis*, the clusters of modified pinnules at the forks look like small Witches' brooms: in *G. pectinata* they are broader and more deltoid than the normal pinnules and have a distinct type of venation. In this connexion the suggestion may be made that some of the *Aphlebiæ* characteristic of the rachises of certain Palæozoic pinnate fronds may be persistent protective structures homologous with those which cover the bud of a *Gleichenia* where the original dichotomous habit has not given place to the pinnate construction.

The monotypic genus *Platyzoma*, an obvious xerophyte, bears tufts of simple or occasionally forked leaves with very small segments associated with much reduced filiform leaves. The New Caledonian *Stromatopteris* has a horizontal rhizome giving off erect branches, repeatedly and irregularly forked, with fronds similar to those of *Platyzoma* but with rather larger segments. *Gleichenia simplex* of the high Andes is exceptional in having unbranched fronds like those of juvenile plants of other species.

The circular naked sori of *Gleichenia* usually have 2 to 5 sporangia, though in some species, e. g. *Gleichenia pectinata*, the sporangia are more numerous. In development the sori belong to the *Simplices* of Bower. In *Platyzoma* the stele is medullated. In *Gleichenia* it is often protostelic, but in *G. pectinata* it is solenostelic. Prof. Bower assigns the family to a position among the more primitive of the Filicales. The *Dicranopteris* section is generally regarded as more primitive than *Eugleichenia*.

It remains to consider briefly the geographical distribution of the family. The subgenus *Eugleichenia* is confined to the Old World: *Dicranopteris* ranges from Japan to the Straits of Magellan and extends as far north in America as Mexico. The approximate limits of distribution are shown in Map A (Pl. 16). *Gleichenia* occurs in the clearings of tropical forests, on the edge of jungles, on tropical alpine peaks, in the heath vegetation on the higher slopes of Ruwenzori, in Mexico, Patagonia, China, India, Australia, and elsewhere. The tangled fronds, their tall and slender rachises with outstretched forking pinnæ, often in company with the genus *Dipteris* on the sun-exposed banks on the hill above Penang, present an impressive picture of tropical luxuriance. Malaya is one of many regions in the tropics and subtropics where the genus is rich in individuals and in species. Underwood describes *Gleichenia* thickets with "tunnels cut through them in which men could walk erect." *Gleichenia* flourishes in the rain forests of Mexico, in

Costa Rica—rich in endemic forms—, in the West Indies, along the Andes to the Falkland Islands, on the heaths of Ruwenzori up to over 10,000 ft., from Natal to Table Mountain, in Madagascar, in the Island of Réunion, on Amsterdam Island, in New Guinea where Dr. Wollaston tells me that he collected several species, some growing at an altitude of over 12,000 ft., in New Caledonia where Prof. Compton recently found at a height of 8000 ft. one of the largest species of the genus, in New Zealand, and as far north as Hawaii, in India, China, Japan, and the Philippine Islands. The absence of *Gleichenia* from Northern Africa, the whole of Europe, Western Asia, and practically the whole of the North American continent is a surprising fact. To this geographical distribution the fossil record affords a striking contrast.

It has long been a palæobotanical commonplace that in the Cretaceous epoch the vegetation of West Greenland would appear to have been sub-tropical; in other words, the plants found in the freshwater sediments exposed on the east coast of Disco Island and in the ravines of the mainland, 300 miles north of the Arctic circle, are in sharp contrast to the vegetation which now flourishes in the short but concentrated summer on the margin of the ancient Greenland plateau buried under an ice-sheet of unknown depth. Twice only have I collected fronds of the Fern *Gleichenia*: on the edge of a Malayan forest where it luxuriates under a tropical climate, and from sediments deposited in a delta or inland lake on the submerged fringe of Cretaceous Greenland. The apparent identity of the living and the dead gives reality to Carpenter's aphorism "we are still living in the Cretaceous period." Hooker in one of his letters expressed the opinion that "Geology gives no evidence of a progression in plants," and adds "I do not say that this is proof of there *never* having been a progression—that is quite a different matter—but the fact that there is less structural difference between the recognisable representatives of Conifers, Cycadeæ, Lycopodiaceæ, etc., and Dicotyledons of the Chalk and those of present day than between the animals of those periods and their living representatives, appears to me a very remarkable fact."

It is easy to speak of the "first appearance" of certain plant types, but actually to trace to its source any family or group is a problem that seems to remain insoluble. The search for origins has much in common with the quest of the Holy Grail. The unfolding of plant-life viewed through the distorting mists over the successive stages of earth-history takes the form of a series of outbursts of energy—the records of one period tell us nothing, while those of the next reveal a fresh type of vegetation, or it may be a single genus in possession of widely scattered regions of the world.

Whatever the process of unfolding may have been, we seem unable to do more than observe the completed results; the beginnings are hidden from us, and the farther we penetrate into the past the farther into the distance recedes the object of our search.

The genus *Oligocarpia*, founded on fern-like fronds from the Coal

Measures, bearing circular sori with a few sporangia which were probably annulate, is often quoted as a probable Palæozoic representative of the Gleicheniaceæ; but the evidence is not conclusive. We can at least state with confidence that fronds of certain Palæozoic Pteridosperms show a scheme of branching apparently identical with that of recent Gleicheniaceæ. In itself this is of no great value in view of the fact that dichotomous branching is probably a primitive feature of plant architecture.

Fossil species of the family Gleicheniaceæ are fairly widely spread in the Northern Hemisphere far beyond the present limits of *Gleichenia*. In early Cretaceous times Ferns hardly distinguishable from existing species belonging both to the *Eugleichenia* and to the *Dicranopteris* sections were particularly abundant in Western Greenland far within the Arctic circle, and specimens from Upper Jurassic or possibly Wealden beds in Spitzbergen have also been referred to *Gleichenites*.

The oldest examples which can be assigned with confidence to the family are from Keuper strata in Switzerland, and a portion of a frond of the *Eugleichenia* type, but with no fertile segments, is recorded from beds of the same age in France. From beds in New Zealand, which may be Rhætic in age, Arber has described specimens as species of *Microphyllopteris*, a name instituted by him as being more appropriate than *Gleichenites* in the absence of proof of affinity to the Gleicheniaceæ. To Arber's genus Walkom refers specimens from the Rhætic of Queensland. Portions of sterile fronds from the Rhætic flora of Franconia bear a striking resemblance to some of the recent species of the *Eugleichenia* type. *Gleichenites* was unquestionably a member of the Lower Jurassic flora of Poland; it is represented by well-preserved fronds, though without fertile pinnæ, in Jurassic rocks in India. Examples are recorded from Upper Jurassic rocks in Sutherland on the North-East coast of Scotland, and from the same beds a fragment of a rhizome was discovered with a protostele of the *Gleichenia* type. From Upper Jurassic, or possibly Wealden, strata in Patagonia *Gleichenites* has been described by Halle. It is, however, in the Cretaceous floras that the genus was especially abundant: good examples are known from several European localities; in West Greenland *Gleichenites* flourished most abundantly. It was also well represented in the Wealden flora of Belgium in which Dr. Bommer tells me he has discovered rhizomes with steles agreeing with those of recent species. Similarly the genus occurs in Lower Cretaceous strata in England, Germany, France, and other European districts including the Balkans; it is also represented in the Cretaceous flora of Sakhalin Island. Comparatively few satisfactory specimens have been found in North America: the best are those on which Knowlton founded the species *Gleichenites pulchella*, showing dichotomously branched fronds with pinnæ thickly set with very small segments, from the Upper Cretaceous of Wyoming. During Tertiary times *Gleichenites* seems to have lingered in Europe; but the records are few and fragmentary.

MATONINEÆ AND DIPTERIDINÆ.

Members of these two families, linked by morphological ties, often grow side by side: Wallace, in describing an ascent of Mt. Ophir in the middle of the Malay Peninsula 50 miles east of Malacca, wrote:—"We emerged into a lofty forest pretty clear of undergrowth" and at a higher level "came out upon the Padang-Batu or stone-field . . . parts of it were quite bare, but where it was cracked or fissured there grew a luxuriant vegetation, among which the Pitcher plants were most remarkable. . . . A few Conifers of the genus *Dacrydium* here first appeared, and in the thickets, just above the rocky surface, we walked through groves of those splendid ferns, *Dipteris Horsfieldii* [= *D. conjugata*] and *Matonia pectinata*, which bear large spreading fronds on slender stems, 6 or 8 feet high." Many years later Mr. Tansley in speaking of the same locality mentions *Gleichenia linearis*, *G. flagellaris* with *Dipteris conjugata* and *Pteridium aquilinum* as the constant associates of *Matonia*. A short distance below the summit of the mountain Wallace collected plants of *Schizæa dichotoma* *.

If we could interpret the mystic utterances of these Ferns of the Malayan mountain as the Priestesses professed to interpret the rustling of the Oak leaves at Dodona, we should hear thrilling stories of world-wide wanderings and glean something of the ancestral history of the members of the company, a revelation which might perhaps confound or elate more than one Hooker lecturer.

DIPTERIDINÆ. The genus *Dipteris*, represented by at least six species, has a creeping rhizome with a tubular stele and reticulately veined fronds varying considerably in the degree of dissection of the lamina. *Dipteris conjugata*, the most widely distributed species, occurs in the Malay region, the Philippine Islands, Formosa, New Guinea, New Caledonia, the New Hebrides, and elsewhere.

A closely-allied species grows in Yunnan. From a slender petiole reaching a height of 7 or 8 feet a broad lamina spreads more or less horizontally, and resembles in habit a large branch of a Giant Hemlock leaf or the broad leaf of a *Petasites*: a deep sinus divides it into symmetrical halves with finger-like serrate lobes. The sori, varying much in size, are often confluent, and are of the mixed type. *Dipteris Wallichii*, of Northern India, has similar leaves, but the ultimate segments are entire. The Bornean species, *D. Nieuwenhuisi*, is smaller though similar in habit. In *D. Lobbiana*, another Bornean fern, the petiole branches at its summit into a series of forked linear pinnæ bearing rows of sori; in this species the sporangial development is simultaneous. The frond of *D. quinquefurcata*, a species with a wider range, is constructed on the same plan but has broader pinnæ.

It is the distinction between the laterally continuous lamina of *D. conjugata*

* Wallace's specimens are in the British Museum Herbarium.

with mixed sori and the *D. Lobbiana* type, represented by pinnæ free to the base and with sori composed of larger simultaneously developed sporangia like those of *Matonia* and *Gleichenia*, which forms the most striking departure from the otherwise very uniform family characters.

MATONINEÆ. *Matonia* is represented by three species—if in opposition to Copeland, whom Christensen follows, we retain the Bornean fern *Matonia sarmentosa*, Bak. in the genus instead of adopting Copeland's generic name *Phanerosaurus*. *Matonia pectinata* has a scale-covered rhizome bearing tall petioles splitting into fan-shaped fronds with comb-like pinnæ spreading radially through more than half a circle; the linear segments are slightly oblique and acute. Its fronds present a striking resemblance in habit to those of some species of *Gleichenia*, notably *G. flabellata*, *G. quadripartita*, and *G. Cunninghamii*. *Matonia pectinata* occurs in Borneo and the Malay Peninsula. *Matonia Foxworthyi* from Borneo has fronds identical in habit, but with obtuse segments set square to the pinnæ. The sori, like those of *Gleichenia*, belong to the Simplicis section. In *Matonia sarmentosa*, confined to one locality in Borneo, the rachis forks repeatedly and gives the frond an appearance very different from that of *M. pectinata*; both branches of a fork may develop more or less equally, or one of them may develop fully while the other ends in an aborted bud. The polycyclic structure of the stele is a peculiar family character.

Though not included in either the Matonineæ or the Dipteridineæ, the two genera *Neocheiropteris* and *Cheiropleuria* call for a brief reference because of their resemblance to *Matonia* and *Dipteris* in frond-habit and in certain other features. *Neocheiropteris pulmatopedata* from Yunnan, regarded by Bower as a *Dipteris* derivative, appears to be identical with *Matonia pectinata* in the forked disposition of the spreading ribs, but, as in *Dipteris*, these are connected by a continuous lamina with a series of distal lobes.

Cheiropleuria bicuspis, which is often associated with *Dipteris conjugata*, extends from the Malay Peninsula to the Luchu Islands, Formosa, and New Guinea. The reticulately veined lamina may be ovate and entire, bicuspid like the leaf of a *Liriodendron* or repeatedly and more deeply lobed. Bower describes it as "a condensed and webbed example of the *Matonia* type."

While certain fossil Ferns are nearer to one or other of the two recent genera *Dipteris* and *Matonia*, at least in habit and venation of the frond, in others characters foreshadowing both living genera are combined. The first series to be considered includes genera which have often been definitely included in the Dipteridineæ; but while this course may be defended, it is preferable to follow Nathorst and refer some of the extinct types to a separate family, the Campopteridineæ, which he suggested might rank as a subfamily of Dipteridineæ. Good as some of the material is, the difficulty of subjecting fossil sporangia and sori to such minute examination as is possible with fresh specimens and the unavoidable incompleteness of the

data on which diagnoses rest stand in the way of precision and thoroughness of comparison. The genera *Dictyophyllum*, *Thaumatopteris*, *Camptopteris*, and *Clathropteris* are the best-known members of the Camptopteridinae; the genus *Hausmannia*, as Halle has recently shown, may safely be more closely associated with *Dipteris*.

Dictyophyllum is represented by many species, not always easily distinguishable, ranging from Upper Triassic to Lower Cretaceous floras. It is characterised by large webbed fronds, with reticulate venation, often borne on long petioles sparsely scattered on creeping rhizomes. Illustrations and descriptions published by Nathorst and by Zeiller show that the fronds of some forms must have exceeded in size those of the largest *Dipteris*, reaching a span of about 2 metres, with individual pinnæ attaining a length of 1 metre. There is considerable range in the lobing of the pinnæ, in the form of the ultimate segments, and in the size of the fronds. In some of the Rhætic species the petiole forked into two equal arms curved outwards and slightly inwards like the limbs of an inverted Moorish arch, each bearing apparently on the outer side, but actually on the twisted inner side, numerous spreading pinnæ. An untwisted *Dictyophyllum*, but for the webbed and reticulately veined lamina, would be practically identical with a frond of *Matonia pectinata*. The sori are crowded and often confluent; the annulus is incomplete. The sporangia are larger, fewer in each sorus, and produced more spores than in *Dipteris*. Mr. Hamshaw Thomas has recently shown that in the Jurassic species *Dictyophyllum rugosum* the sporangia are not in definite sori but scattered over the surface of the frond, agreeing in this respect more closely with the recent genera *Platyserium* and *Cheiropleuria* than with *Dipteris*. In the Rhætic species the sori are of the Simplicis type. Mr. Thomas concludes that *Dictyophyllum* and other related Mesozoic Ferns "should be considered as closely allied to the modern Dipterid ferns."

Thaumatopteris. This genus is similar in habit and range to *Dictyophyllum* and may perhaps be regarded as a subgenus. For our immediate purpose the differences between the two types are unimportant.

Camptopteris. In the Rhætic species, *C. spiralis*, Nath., from the South of Sweden, the spiral twisting of the arms of the petiole is carried further than in *Dictyophyllum*, with the result that the long and narrow pinnæ are attached along a spiral line. In another species, *C. serrata*, Kurr, the habit of the frond conforms to that of *Matonia pectinata*.

Clathropteris. The serrate strap-shaped pinnæ, which may reach a length of 80 cm, are given off from two arms of the petiole; at the base the laminae and the fan-like group of pinnæ are united and the main ribs form a *Matonia*-like pattern. The rhizome agrees closely with that of *Dictyophyllum*.

Hausmannia. The more completely webbed fronds of this genus are in some species indistinguishable in habit, as in venation, from those of some examples of *Dipteris*. A fortunate discovery of well-preserved fertile

specimens in Lower Jurassic strata in the Island of Bornholm has enabled Halle to demonstrate a very close agreement with *Dipteris* in the structure and spore-output of the sporangia.

To the Matonineæ it is customary to assign the fossil genus *Laccopteris*, a type agreeing in habit and in the structure of the sporangia with *Matonia*. The presence of an indusium has not been demonstrated, but in view of the detachable nature of the soral covering in *Matonia*, little weight can be given to negative evidence. In the pinnules of *Laccopteris* the veins are more fully anastomosed than in *Matonia*, but in this respect there is considerable variation.

Fossil fronds agreeing still more closely with those of the recent genus are referred to *Matonidium*, and some of these cannot be generically distinguished from *Matonia pectinata*. The discovery of rhizomes of a Wealden species of *Matonidium* in Belgium with the characteristic polycyclic stelar structure afforded welcome confirmation of the close affinity of the fossil to the recent Ferns. The Belgian specimens will, it is hoped, soon be described in detail by Dr. Bommer. Some of the fronds of *Matonidium* from Jurassic and Wealden rocks in England and other countries differ from those of the recent species in the greater production of sori and in the larger number of sporangia in each sorus.

Fossils from Rhætic beds in Franconia and Sweden described as species of the genera *Andrianea*, *Guthiera*, and *Solenocarpus* agree in habit with *Matonia* but differ in the form of the sori.

Reference may also be made to certain fossil fronds described under the name *Nathorstia*: in habit as in venation and form of the pinnæ this genus is indistinguishable from *Laccopteris*, but the examination by Nathorst of fertile specimens from Cretaceous strata in Western Greenland and by Halle of material from Upper Jurassic, or Wealden, beds in Patagonia has failed to demonstrate the occurrence of annulate sporangia. The circular sori appear to consist of radially disposed synangia which the authors compare with the sori of the Marattiaceous genus *Christensenia* (= *Kaulfussia*), though in detail there are certain differences. Unfortunately specimens collected last year by Mr. Holttum and myself in Greenland, though supplying some new facts, did not throw any light on the structure of the sori. The available evidence does not entitle us to assign *Nathorstia* to the Dipteris-Matonia alliance; nor, on the other hand, am I convinced that the soral characters justify inclusion in the Marattiaceæ. It is noteworthy in this connexion that we found well-preserved, fertile *Laccopteris* fronds in the Cretaceous plant-beds of Greenland.

Weichselia, a fern with large fronds and short linear pinnules with anastomosing veins which is characteristic of Wealden or Lower Cretaceous floras in several parts of Europe, probably represented in the Cretaceous flora of Egypt and recently discovered in Wealden beds in Peru, calls for a brief

reference. In a preliminary account by Dr. Bommer of the morphological features of specimens of *Weichselia* discovered by Father Schmitz at Bernissart in Belgium—a locality rendered classic by the wonderful assemblage of *Iguanodon* skeletons—it is shown that in the structure of the stem and petioles, the habit of the fronds, and in the organisation of the sori there is a close resemblance to *Matonia*. Dr. Bommer thinks that in a less degree the sum of characters suggests comparison with the Marattiaceae.

Mr. Berry has figured some fern fronds, unfortunately sterile, from the Potomac Formation of Eastern America under the name *Knorltonella Maxoni*, which he refers to the Matonineae. The fronds are described as pseudodichotomous, at least in part; the pinnules are linear-lanceolate and the rachis is winged. No anastomosis of the lateral veins could be seen. This American fern resembles a Cretaceous species, *Phlebomeris spectanda*, figured by Saporta from Portugal, but neither affords convincing evidence of close relationship to *Matonia*.

Map B (Pl. 17) is intended to present in broad outline the geographical distribution of members of the Dipteris-Matonia alliance treated collectively; it does not show the range in space of each genus. It is, however, important to consider briefly some of the data collected in the course of a general review of the geological records.

It is not my aim to connect the Mesozoic records with the Palaeozoic: between the two there appears to be a wide gulf. Among the numerous fronds of Pteridosperms and Ferns in the Upper Carboniferous and Permian strata there are indications, both in vegetative and reproductive characters, of possible connecting-links between the different phyla of Lepto-sporangiate Ferns which assumed a dominant position in the Rhetic and Jurassic periods. The difficulty of making direct contact between the age of Pteridosperms and the succeeding age of Ferns may be largely due to the difficulty of determining whether a Palaeozoic fern-like frond should be classed as a Pteridosperm or a true Fern, but on the other hand the relationship between the two ages may not be as close as it is usual to assume. In the latter part of the Triassic period we seem to pass with remarkable suddenness to a new phase of plant evolution; the old order gives place to the new; one cycle is completed and another has begun. This transformation in the plant-world may be intimately associated with some far-reaching event in the physical history of the earth's crust. It may well be that crustal foldings in the latter part of the Palaeozoic era and the prevalence of desert or semi-arid conditions over wide regions during a part of the Triassic period were factors which influenced the progress and direction of plant development.

The genus *Camptopteris*, if not the oldest, is one of the earliest representatives of the Dipteris-Matonia line; it occurs in the rich Upper Triassic plant-beds of Lunz in Austria, the flora of which has never been adequately described. It occurs also in Upper Triassic beds in Würtemberg. The

large fronds of *Camptopteris spiralis* described by Nathorst are from the rich Rhætic strata in Scania.

Dictyophyllum would seem to have attained its maximum development, as measured by size of frond and range of form, in the Rhætic period: this is clearly shown by the wonderful specimens figured by Zeiller and Pelourde from Tonkin and by Nathorst from Southern Sweden. The genus was also well represented in the Rhætic flora of Franconia. The line between Rhætic and Jurassic floras cannot readily be drawn. For present purposes the floras of the localities enumerated may be classed together: *Dictyophyllum* and *Thaumatopteris* are practically absent from Rhætic-Jurassic floras in North America, but *Dictyophyllum* is recorded from Alaska. *Dictyophyllum*, sometimes also *Thaumatopteris*, occurs in many localities in Europe, from England to Poland, Sardinia, and Russia, in Scania and the Island of Bornholm; in Chile and the Argentine, China and Japan, Queensland and New Zealand; also in Graham Land on the edge of Antarctica; in Persia and Afghanistan. Nathorst speaks of thousands of fronds of *Dictyophyllum* in the plant-beds of Southern Sweden, and sees in the diversity of leaf-form evidence of a centre of development. It is remarkable that the two regions of greatest development of this type of fern would seem to have been Tonkin and Scania, though it may be that the greater richness of the Rhætic flora in these two areas is due to conditions unusually favourable for fossilisation.

Cluthropteris. The genus is represented in the Upper Triassic flora of Lunz and by very large fronds in beds assigned to the same horizon in Virginia. It occurs in Rhætic beds in Scania, Russia, Tonkin, and China; also in Jurassic strata in several European localities. One imperfect specimen referred with some doubt to this genus was found in rocks in Egypt which may be Cretaceous in age.

Hausmannia. This, the genus nearest to *Dipteris*, is represented by some imperfect specimens in the Rhætic beds of Scania; by several well-preserved fronds in the Rhætic-Liassic strata in Bornholm; also in Liassic beds in Austria. An imperfect specimen from Jurassic strata in Alaska has been referred to *Hausmannia*. The genus is widely spread in Upper Jurassic, Wealden, and Lower Cretaceous rocks in England, the North-East of Scotland, Belgium, and France, and is especially abundant in Lower Cretaceous beds at Quedlinburg in Germany. *Hausmannia* is probably a later offshoot from the parent stock than the genera of the *Camptopteridinae*.

Laccopteris is represented by well-preserved fertile specimens in the Rhætic floras of France and Franconia. The oldest are from the Upper Triassic beds of Lunz. It is characteristic of Jurassic floras in Europe and is recorded from Cretaceous rocks in Western Greenland.

Matonidium occurs in several Middle Jurassic floras, in Wealden beds in England, Belgium, Germany, Russia, and other countries, and a species

hardly distinguishable from *Matonia pectinata* or *M. Foxworthyi* has been described by Krasser from Lower Cretaceous rocks in Moravia. Specimens, which leave much to be desired in the quality of the material, are recorded from the Cretaceous of Colorado and from other localities in the United States. It would seem that the Matonineæ were not prominent members of American Mesozoic floras, but they flourished abundantly in the Jurassic and earlier Cretaceous floras of the New World, extending as far north as approximately lat. 70° N. in Greenland.

The problem of the original home of the Dipteris-Matonia stock is not easy of solution. When the fossil forms first appear among the records of the rocks, certain genera had already reached a vigorous stage of development in Europe and North America; by the Rhætic period they were thoroughly established in the Tonkin region, also in Germany and Scania. The oldest known genera had fronds of the more completely webbed type and were reticulately veined, while such genera as *Laccopteris* and *Matonidium* seem to have persisted as vigorous types to a later period. There is no good reason to suppose that this alliance was more widely represented in Tertiary floras than it is at the present day.

SCHIZÆACEÆ.

Within this family there is a very wide range in the habit of the fronds as represented by the four genera *Schizæa*, *Aneimia*, *Lygodium*, and *Mohria*: the apical annulus, usually of a single row of cells, and the occurrence of the sporangia singly and not in regular groups are constant characters. A simple protostele characterises the stem of *Lygodium*, while other genera possess both the solenostelic and dialystelic types of vascular cylinder. In several species of *Schizæa* the fronds are slender and filiform like thin blades of grass or the cylindrical leaves of a *Juncus* with clusters of sporangia in monangic sori on the reduced lamina at the tips of the fronds: in other species the frond resembles a much dissected leaf of *Ginkgo*. The genus has a remarkably wide range in the southern hemisphere, and *Schizæa pusilla* extends as far north as Newfoundland (Map (c) (Pl. 18)). *Aneimia*, represented by several species in South America, occurs also in Mexico and Texas, the Falkland Islands, Abyssinia, South Africa, and India. The fronds are usually divided into three branches at the base, the two lateral pinnæ being fertile with reduced laminae, and the sterile pinnæ bear segments varying considerably in shape and in the degree of dissection. *Lygodium* is characterised by a rachis of indefinite growth which behaves as a liane and reaches a length of 100 ft., giving off dichotomously branched linear pinnæ bearing marginal spikes of sporangia. This genus extends from Mexico to Rhodesia, South China, Queensland, New Zealand, New Caledonia, and Japan. The genus *Mohria* is represented in South Africa, the Zambesi region, and on Kilimanjaro. An aberrant species from Brazil, one of several xerophytic examples

of the genus, *Aneimia* (*Trochopteris*) *elegans*, bears a rosette of small spatulate leaves with sporangia on the under side of the lower portion of the fronds.

From the Triassic-Rhætic floras there are fewer records of this family than of the Dipteris-Matonia Ferns. One of the oldest examples has recently been described by Gothan under the generic name *Norimbergia* from Rhætic beds in the neighbourhood of Nürnberg: the characteristic sporangia are clearly preserved. Fossil pinnæ bearing sporangia identical with those of existing species are recorded from Jurassic rocks of England, Sardinia, Afghanistan, Korea, and elsewhere: the majority of the fossil forms are included in the genus *Klukia*, which has bi-pinnate or tri-pinnate fronds with small linear pinnules differing in habit from all living members of the family. *Klukia* occurs also in Wealden rocks: the discovery of fertile specimens in Peru points to the probability that sterile fronds described as a species of the provisional genus *Cladophlebis* from Wealden beds in England and other parts of the world may belong to *Klukia*. Another type of Schizæaceous fern characteristic of Lower Cretaceous floras is *Ruffordia Gœpperti*, recorded from England and Germany and other districts in Europe. This fern has recently been described in detail by Halle from fertile specimens discovered in presumably Wealden strata in Russian Manchuria. *Ruffordia* closely resembles in habit some recent species of *Aneimia*. Under the name *Schizæopsis* Mr. Berry has described fertile specimens of fronds from the Potomac Formation of Virginia which in habit bear a very close resemblance to species of *Schizæa*, e. g. *S. elegans*, with a lamina deeply dissected into narrow strap-shaped segments. This discovery is of special interest, as it suggests the probability that some of the leaves from other Lower Cretaceous or Jurassic floras which it has been customary to refer to the genus *Baiera*, a member of the Ginkgoales, may be sterile fronds of ferns closely allied to *Schizæa*. It is, for example, not improbable that some of the specimens from Jurassic rocks in Siberia described by Heer as species of *Baiera*, but which are slightly different from the typical representatives of that genus, may be Schizæaceous ferns.

Various leaf fragments from Tertiary beds have been included in the genus *Lygodium*, and there is no doubt that this genus was a member of some of the European floras of that period.

The Carboniferous genus *Senftenbergia* is often quoted as a Palæozoic member of the Schizæaceæ because of the presence on the small fertile linear pinnules of sporangia with an apical annulus composed of 4 to 5 rows of thick-walled cells, but in view of differences of opinion on its affinity and having regard to our lack of knowledge of the morphological features of the plant to which the fronds belonged, it would be rash to assume a direct relationship of this Palæozoic genus to the existing genera of the Schizæaceæ.

MARATTIACEÆ.

This family of Eusporangiate Ferns includes the genera *Angiopteris*, *Archangiopteris*, *Marattia*, *Danæa*, *Macroglossum*, and *Christensenia*. In their thick fleshy stems, the large stipules, and in the soral characters these genera are in marked contrast to those already described. *Marattia* occurs in the tropics of the East and West hemispheres; *Angiopteris* is widely spread in the Eastern tropics in Malaya, India, Ceylon, Formosa, and Tabiti. *Angiopteris* includes species with the tri-pinnate fronds 12 ft. long with pinnæ 4 cm. broad and 30 cm. long, bearing short linear sori of separate sporangia. In the Bornean genus *Macroglossum*, with fronds of the *Angiopteris*-type, the pinnæ are broader and longer and the sori contain more sporangia. It is noteworthy that this genus of restricted range is very similar in the characters of its fronds to some of the widespread Rhætic species assigned to *Marattiopsis* or *Danæopsis*. Certain species of *Marattia* closely resemble *Angiopteris* in habit, but occasionally the larger pinnæ show a tendency to subdivision into small segments, while in other species the ultimate segments are only a few millimetres in length. In *Marattia* the sporangia are united into woody capsular synangia. *Archangiopteris* from Southern China has pinnate fronds with segments like those of *Danæa*, but the sori except in their greater length are like those of *Angiopteris*. The greater length of the linear sori is a character met with in fossil Marattiaceous fronds from Rhætic beds. *Danæa* is confined to tropical America; the fronds are simple or pinnate and the elongate sori extend from the midrib almost to the edge of the lamina. The parallel rows of sporangia are united into compact masses by union with them of tissue which grows up from the fertile lamina. Costa Rica possesses a species of *Danæa* with delicate and relatively small leaves in texture like those of a filmy fern. The genus *Christensenia* from the Philippines differs from all others in its palmate leaves resembling those of a Horse Chestnut and in the peculiar circular sori. The disposition of the main ribs recalls the habit of *Matonia pectinata* and *Neochiropteris*.

Omitting the fern-like fronds from Upper Palæozoic floras which in the characters of the sori appear to resemble those of existing Marattiaceæ more closely than the Leptosporangiate ferns, the oldest examples of fronds with fertile pinnæ agreeing generally in habit with *Angiopteris*, *Macroglossum*, and *Archangiopteris* are from Upper Triassic beds in Switzerland, Austria, and France. An excellent account of Palæozoic Ferns is given by Dr. Scott in the last edition of his 'Studies in Fossil Botany' in which he describes several 'species which reveal both in soral characters and in anatomical structure obvious points of contact with the Marattiaceous type. He quotes the genus *Asterotheca* as a Palæozoic fern which persisted into the Triassic and even Rhætic period. It is, however, in the older Mesozoic rocks that we

first encounter Ferns which agree closely in habit as also in the characters of the sori with recent representatives of the family (Map D) (Pl. 19).

Specimens were referred to the Marattiaceæ by the late Prof. Zeiller from Triassic rocks in Madagascar. Ferns of similar type, with long strap-shaped pinnæ, described either as species of *Marattiopsis* or *Danæopsis* are abundant in Rhætic floras; they occur in Scania, India, Tonkin, South Africa, Australia, and elsewhere. It has recently been demonstrated by Halle that the sori of a Rhætic species of *Danæopsis*, *D. fecunda*, consist of contiguous but separate sporangia covering the under side of the lamina on each side of the midrib: as he states, the comparison of *Danæopsis* fronds of this type with those of the genus *Danæa* is entirely unwarrantable as the sporangia are of the Angiopteris type.

Marattiaceous fronds with fertile pinnæ of linear form are common in Jurassic beds: they are recorded from England, Scania, Bornholm, Poland, India, China; and a fern of different habit, but with sori suggesting comparison with those of some recent Marattiaceæ, has been described from Jurassic rocks in Afghanistan. A few ferns from Jurassic and Cretaceous strata in North America have been recorded under the names *Danæopsis* and *Angiopteridium*; but especially in the case of the latter genus the specimens are sterile and afford no definite evidence of affinity to the Marattiaceæ. Fertile pinnæ from the Jurassic plant-beds of Oregon described as a species of *Danæopsis*, characterised by linear sori of separate sporangia but without any indication of actual structure, may belong to the Osmundaceæ: the pinnæ agree closely with those of the well-known form *Cladophlebis denticulata*, some examples of which are certainly Osmundaceous.

There are a few records of Marattiaceous ferns from Cretaceous and Tertiary floras, but the maximum development of the family as we now know it seems to have been in pre-Cretaceous times.

CONCLUSION. In conclusion I have to confess that the very incomplete retrospect based on a selection from the fragmentary documents in the earth's crust leads to no very definite conclusion. Darwin in a letter to Hooker in 1869 wrote "At each epoch the world tends to get peopled pretty uniformly, which is a blessing for Geology." The comparative uniformity of the world's vegetation in its general composition at certain stages in the history of the earth is a fact helpful to the historical geologist in arranging his chapters. It has, however, a significance from the point of view of evolution which may be fundamental. "In these books of stone we find the soul of history"; but the problem is to recognise the soul when we find it. Over vast areas whole communities seem to have appeared and disappeared simultaneously. Beneath this exaggerated statement there is an underlying truth. As Suess says, "It is the organic remains, no doubt, which afford us our first and most important aid in the elucidation of the

past. But the goal of investigation must still remain the recognition of those great changes, in comparison with which the changes in the organic world would only appear as phenomena of the second order." It is generally agreed that the Leptosporangiate Ferns became clearly defined as a class, and assumed an important rôle in the drama of plant-life subsequent to the Palæozoic era.

Ferns existed in the forests of the Carboniferous-Permian epoch, but their precise relationship to existing types is not clear: the opinion may be hazarded, rash though it is, that the selected representatives of Mesozoic Ferns mentioned to-day are not directly connected by descent with Palæozoic ancestors.

Between the shales and seams of coal rich in the remains of the luxuriant vegetation of the late Palæozoic forests and the sun-cracked mud and barren sandstones of the Triassic period on which some of the early Dinosaurs left their footprints there is a difference which marks the parting of the ways. In the Eastern region of North America on the site of the yet unborn Appalachian mountains, as in other parts of the world, a period of prolonged sedimentation in Palæozoic ages was followed by crustal foldings and retreat of the seas: the trough of an ocean filled with thousands of feet of sedimentary material was converted into a lofty range of mountains. This "Appalachian revolution," as it has been called by American geologists, was "one of the most critical periods in the history of the earth." It is the physical expression of the beginning of a fresh cycle in the inorganic as in the organic world. In England the hummocks of Archæan rock in Charnwood Forest polished by wind-blown sand of Triassic deserts enable us to picture the arid wastes and salt-covered beaches of inland seas, to reconstruct the scenery familiar to the "clumsy reptiles" of the early Mesozoic age in both the Old and New Worlds. In Virginia, in the district of Lunz in Austria, and in some other parts of Europe sediments rich in plants demonstrate the occasional prevalence of conditions favourable to vegetation during the latter part of the Triassic period, but for the most part the climatic conditions of the continents would seem to have been in striking contrast to those associated with the very luxuriant development of the Permo-Carboniferous vegetation. The revolution in the earth's crust with the concomitant interchange of land and water must have had its reflex in the organic world: land-connexions were made and destroyed, the factors governing climate were reshuffled, and the balance of life seriously disturbed. It is not merely missing chapters that give the impression of discontinuity in the history of life. The apparently sudden change in the general facies of the plant-world is the expression of an almost catastrophic adjustment to a new condition of stability in the crust of the earth.

As new lands emerged from the sea, new lines of evolution may have been inaugurated; the transmigration of marine plants which Dr. Church

conceives as a single act may have been recurrent. It may be that we shall never piece together the links in the chain of life, not because the missing parts elude our search, but because the unfolding of terrestrial life in all its phases cannot be compared to a single chain. Continuity in some degree there must have been, but it is conceivable that plant-life viewed as a whole may best be represented by separate and independent lines of evolution or disconnected chains which were never united, each being initiated by some revolution in the organic world.

From the Triassic period to the advent of the Flowering plant Ferns were abundant and widely spread; they were a prominent feature in a cycle of evolution which succeeded rather than sprang from the very different vegetation of the Palæozoic era.

In India and other parts of the ancient continent of Gondwana Land the geological succession from the Permo-Carboniferous to the Triassic and Jurassic periods is more gradual and complete, and the conditions under which the strata were deposited more uniform. The southern Palæozoic floras are relatively poor in the variety of types as compared with the corresponding flora in the Northern Hemisphere; their most characteristic genera do not occur in the typical Permo-Carboniferous vegetation of the North. There is no sufficient reason at least as yet to warrant the assertion that the Gondwana continent was the birthplace of ferns which in the early Mesozoic period spread from one end of the world to the other.

In the Rhætic period the floras of Southern Sweden and of Tonkin were especially rich in certain genera of ferns, and identical or closely allied species flourished in both regions. Which of these two centres is nearest to the original home of such ferns as *Dictyophyllum* and its associates? Which of these widely sundered areas was first occupied by the wealth of vegetation discovered in the rocks? To the first question there seems to be no satisfactory answer. While both floras are assigned to the same geological period it is safe to assume that they were not contemporaneous, though which is the older we do not know.

There can be no doubt that the genera *Matonia* and *Dipteris* belong to a section of the Filicales which in former days rivalled in its geographical range the cosmopolitan Bracken Fern of to-day: their present restricted range is not an indication of relatively recent origin. Similarly the geological record clearly establishes the fact that the other genera we have briefly considered, though still vigorous and widely spread, were formerly inhabitants of many parts of the world in which they are now unknown. The facts of geographical distribution must be considered together with distribution in time: among the Ferns at least vigorous development and rapid spread coincide with the earlier stages of their careers, whereas restricted or discontinuous distribution at the present time are best interpreted as evidence of declining vigour or as an expression of inability to hold their own in competition with more recent products of evolution.

The wide distribution in the Northern Hemisphere of Mesozoic Ferns, linked by different degrees of affinity to the families we have considered, in contrast to the prevalence to-day of these families in the Southern Hemisphere suggests comparison with the transtropical wanderings of northern genera when the gradual lowering of temperature which heralded the Pleistocene Glacial period was the compelling factor. In the Northern Hemisphere at least there is no evidence of a general Glacial period in the Mesozoic era. If in pre-Tertiary days there was a similar exodus from North Temperate or even Arctic regions, some driving force other than the pressure of glacial conditions must have been involved. The point I would make is this: do the facts support the assumption that during the Mesozoic era the tendency of plants, or more especially Ferns, was to seek new homes in the South? The hypothesis of a southern migration has often been suggested for earlier as for later periods, and Wieland goes so far as to assert that a boreal centre of creation—using the word in a strictly scientific sense—is “an established certainty.” Let us take two illustrations: the Cretaceous flora of Western Greenland was particularly rich in members of the *Gleicheniaceæ*: the Rhaetic flora of Southern Sweden was characterised by a wealth of development of ferns allied to the *Dipteridinae*.

At first sight it may appear inconsistent with geological data to assume a northern origin for the *Gleicheniaceæ* because pre-Cretaceous species of *Gleichenites* are recorded from localities far south of the Arctic Circle where they occur in strata older than those in Greenland. In Western Greenland there is no evidence of any submergence of the Archæan mainland, not even of the fringe of it, in early Mesozoic times. Plants no doubt flourished on the land, but no sediments were accumulated that earth movements have rendered accessible to us.

The absence of *Gleichenites* has not necessarily a special significance: the genus may have been represented but not preserved. While a northern origin for the family is not entirely ruled out, it cannot be said that the facts warrant the conclusion that the *Gleicheniaceæ* began their career on an Arctic continent; they may have spread from some centre in Southern Europe.

Reference has already been made to the rival claims of Scania and Tonkin to be regarded as one of the earlier centres of development of the *Dipteris* type of Fern. On the whole I am disposed to think that it was from Scandinavia and other northern regions that Tonkin derived its flora.

Whatever view we may hold on the degree of direct relationship between the Palæozoic and older Mesozoic floras, it is difficult to believe that the Gondwana continent was the ancestral home of the great majority of the Ferns which colonised with conspicuous success the Northern Hemisphere. The Permo-Carboniferous Glacial period had its effect upon the vegetation, and it is unlikely that the conditions were such as to favour the production of more than a very few new forms which afterwards played a leading part in

northern floras. If the early Mesozoic Ferns came from Palæozoic ancestors it is much more probable that they were the descendants of plants which formed part of the rich northern flora.

Whatever may have been the main trend of migration, and wherever the ancestral homes may have been, such Ferns as *Gleichenia*, *Dipteris*, and *Matonia* are impressive examples of constancy in a changing world ; in the course of their wanderings from one part of the earth to another they have suffered but little change since the days which preceded the mysterious rise to ascendancy of the Flowering plants.

Continental areas repeatedly shifted and land and sea changed places : it needs no geological knowledge to grasp the fact that the rocks accessible to investigation cannot give us all the clues we seek. Parts of old continents remain ; others are beyond our reach.

“ In some green island of the sea,
Where now the shadowy coral grows
In pride and pomp and empery
The courts of old Atlantis rose.”

Mr. G. M. Trevelyan, contrasting our very imperfect knowledge of Shakespeare himself and what we know of his works, says—“ For however many thousands of years descendants may last, neither we nor our remotest descendants will ever see into the Mermaid Tavern. Its doors are closed, its windows shuttered. Time Past has got the key, and our scholars can only sweep the doorstep.” There is consolation in the fact that among the sweepings there is still treasure to be found.

EXPLANATION OF THE PLATES.

PLATE 16.

MAP A. Distribution of *Gleicheniaceæ*.

PLATE 17.

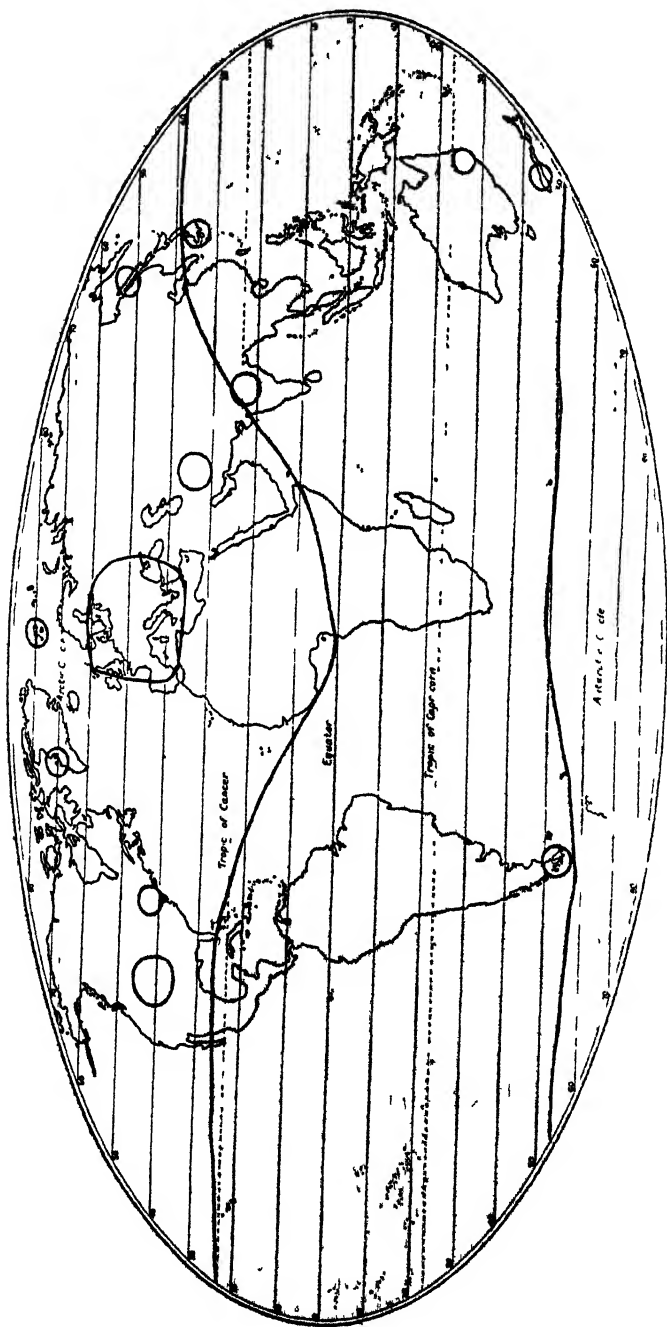
MAP B. Distribution of Ferns of the *Dipteris*-*Matonia* alliance.

PLATE 18.

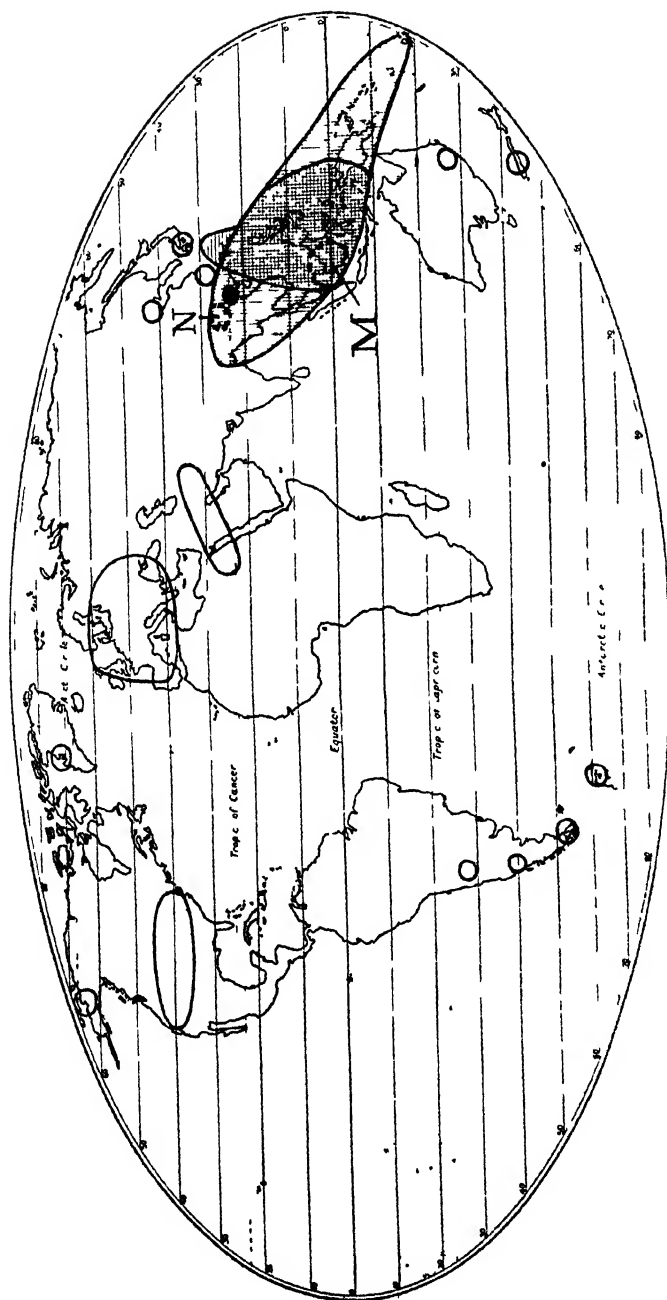
MAP C. Distribution of *Schizæaceæ*.

PLATE 19.

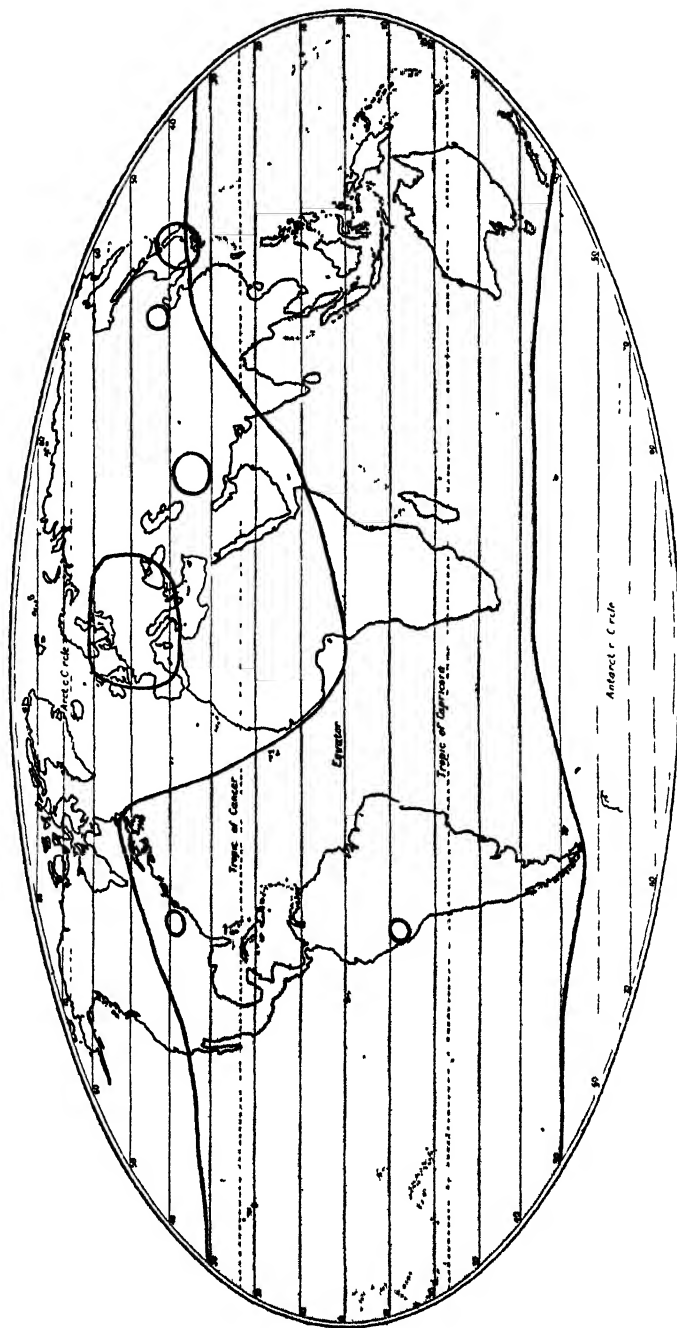
MAP D. Distribution of *Marattiaceæ*.



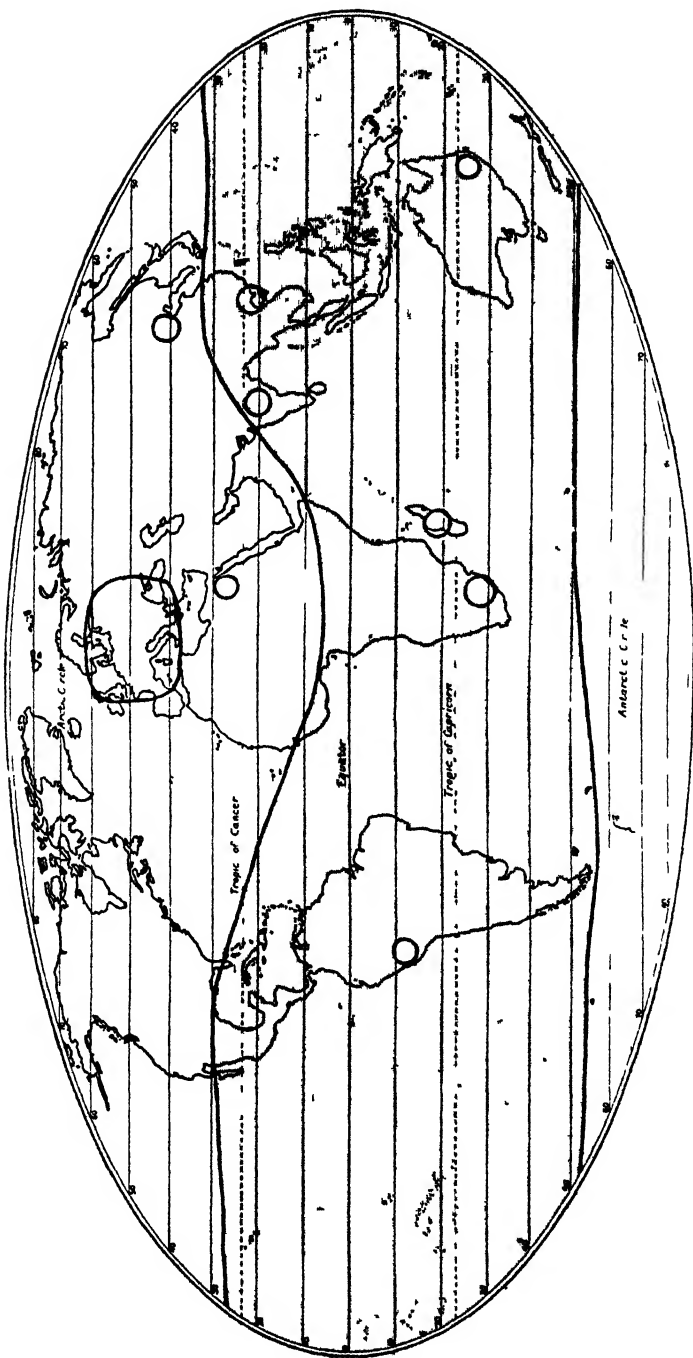
MAP A. GLFICHENIACEÆ. The shaded area shows approximately the present limits of distribution of the family. The localities where Mesozoic representatives have been found are within the enclosed unshaded areas.



MAP B Ferns of the *DIPTERIS-MATONIA VITATA* F. The area indicated by vertical lines is approximately that now occupied by *Dipteris*, the horizontal lines show the distribution of *Chenopodium*, the area M within the dotted boundary is that occupied by *Matonia*, the area N shows the home of *Aechmea*. The other areas including the Toulon region (black dot), enclosed localities from which Mesozoic Ferns mentioned in the text have been obtained



MAP C. SCHIZÆACEÆ. The approximate limits of distribution of the recent species are indicated by the shading.
The localities where Mesozoic representatives have been found are within the enclosed unshaded area.



MAP D MARATTIACEÆ The shaded and unshaded approximately the present distribution of the family. The localities which have yielded Mesozoic species are within the enclosed unshaded areas.

A Preliminary Paper on the Cuticular Structure of certain Dicotyledonous and Coniferous Leaves from the Middle Eocene Flora of Bournemouth.

By HELENA BANDULSKA, A.R.C.S., M.Sc.Lond. (Communicated by Dr. MARIE C. STOPES, F.L.S.)

(PLATES 20 & 21, and 1 Text-figure.)

[Read 18th January, 1923.]

INTRODUCTION.

SINCE very few Angiospermous fossils are preserved as petrifications apart from secondary wood, we are very much at sea as regards the systematic position of most of the abundant and beautiful impressions of leaves which are so characteristic of some of the British Tertiaries. Although these Tertiary leaf-impressions and casts belong to a period too late to give us any clue as to the origin of Angiosperms, they show such enormous differences among themselves, that they should be of great value in determining problems of plant distribution, etc. once they can be definitely identified and compared.

This paper describes Tertiary species which show cuticular structure, and although we cannot take anatomical evidence alone as a criterion of identity, we are justified in combining anatomical characters with external form for this purpose. Data obtained from external form alone are extremely unsatisfactory, the task of identification being usually a hopeless one, for the variety of leaf-forms is apparently endless and the fossils so often fail to show any reliably distinctive features.

In certain cases leaf-impressions possess a cohesive film consisting of the mummified cuticle of the leaf, which is capable of detachment by flaking off with a sharp knife. It is found then that while the internal cells always form a decayed mass, the more resistant external tissue persists uninjured and can be cleared by chemical means so as to reveal the cuticle in as perfect condition as though it were that of a plant existing to-day, and by this method data are yielded for comparison and identification. Leaves susceptible to this treatment are found in the Bournemouth floras, though in other Eocene floras the plants are usually not preserved in this mummified condition, hence the Bournemouth plants furnish a unique opportunity for anatomical investigations along these lines, and the present paper embodies some of this work. The material was partly collected by the writer *in situ*, some supplied by Dr. Marie Stopes from her collection, and the rest is contained in the British Museum collection. The material collected

by the writer was found in Durley Chine, and between Durley Chine and the West Cliff lift, and thus belongs to the Bournemouth Fresh-Water series.

HISTORICAL.

Our knowledge of the Bournemouth Eocene Floras rests mainly upon the work of J. S. Gardner (1883-1886, partly carried out in conjunction with Baron Ettingshausen (1879-1882). Gardner considered the fresh-water series of the Bournemouth Beds to be stored with the most rich and extensive flora yet brought to light from any Tertiary formation. The plants were found mainly in the clays, especially the light coloured clays, and were believed by the investigator to represent a facies chiefly Australian and tropical American. In their joint monograph, Gardner and Ettingshausen (1879, p. 3) point out that the flora is quite a distinctive one of Middle Bagshot age and they believe it to correspond with the subtropical American flora of approximately the same geological period, and suggest that the relationship is an indication that a land connection existed during Middle Bagshot time between England and America. Many generic resemblances were found between the English and American plants, but they also discovered many plants peculiar to the English strata.

Osborne White (1917, p. 21) says: "Usually impressions only of the leaves are met with, but in some cases the substance is preserved showing the variations in texture and even faint indications of autumnal colouring. The flora includes representatives of dicotyledonous forest trees, conifers, ferns, palms, marsh vegetation, and parasitic fungi." Clement Reid (1898) and Osborne White give a resumé of Gardner's observations on the plants found in the cliff-sections, and add little or nothing to his work on the flora.

GEOLOGICAL DESCRIPTION OF THE BEDS.

The cliffs which comprise the Bournemouth fresh-water beds and in which the plant-remains described in this paper are found, extend from Canford Cliff to the east of Bournemouth pier. Their average height is about 100 ft. and they are much cut by chines. J. S. Gardner (1882) divided the Bagshot beds of this district into Upper, Middle, and Lower, and considered them to be mainly of fluvial or estuarine origin. The rocks formerly described as Middle Bagshot Beds are now, in the Hampshire basin, referred to the Lower Bracklesham Beds (Lutetian) and the Upper Bracklesham Beds (Auversian) respectively. The Bournemouth fresh-water beds thus appear to represent the lowest local member of the Bracklesham Beds, the overlying marine strata being referred to the Zone of *Nummulites larigatus* (Lutetian) passing upwards into the Boscombe Sands etc., representing the Zone of *Nummulites variolarius* (Auversian). Mr. Osborne White describes the Bournemouth fresh-water beds as a complex of white and yellow sands,

laminated carbonaceous clays and loams and thin impure pipe-clays arranged for the most part in overlapping lenses of all sizes up to a few hundred yards in diameter. He states that "Physically the fresh-water beds of the Bournemouth Series conform to the delta type of deposit." Gardner considered that the river which deposited these beds flowed from the west in a south-easterly direction somewhat parallel to the inland direction of the chines, depositing its sediments at the very base of the Middle Eocene formations. Clement Reid pointed out how greatly the plants vary in the different lenticular masses of clay in which they occur so that they appear to have been deposited in very small basins formed by backwaters of the river, which was apparently constantly changing its channels.

Isolation and Clearing of the Cuticles.

The leaf material was cleared either in concentrated nitric acid and chlorate of potash, or when this treatment was found too drastic, in Eau de Javelle, which acts more slowly, and was then washed with 20 per cent ammonia. For full details of methods of treatment see Nathorst (1908), Bather (1908), and Thomas (1912). For mounting these preparations of cuticle, water stains followed by glycerine and glycerine jelly were always found more successful than spirit stains followed by absolute alcohol, clove oil, and balsam. Attempts to differentiate cells by staining were not extremely successful. The guard cells of the stomata stained a little more deeply than the ordinary epidermal parenchyma, but all chemical differences in the various types of epidermal structures evidently became obliterated on fossilization. Methyl green, methylene blue, and safranin were found to give the best results in sharply delimiting the cells. For comparison with the fossil leaves, very numerous preparations of recent leaves were made, and the procedure followed was exactly the same in the two cases, so that any post-mortem changes would be similar and comparable. Among the various leaves selected for examination, some of the genera described in Gardner's paper were dealt with first, in the hope that the anatomical structure of the cuticles would confirm the accuracy of the identifications which were based on the external characters of these leaf-forms. The diameters of the cells in the various leaves were measured by means of Hutchinson's Co-ordinate Micrometer and a stage micrometer. It was found that within the limits of the writer's observation, different species of a single genus showed very similar cuticular form: thus certain genera, e. g., *Salix*, *Quercus*, *Fagus*, could be readily identified.

There is not yet a definite consensus of opinion as to what we are to consider really critical characters in epidermal tissues. Thus, for example, in fossil Cycadophyta sinuation of the wall is shown to be a diagnostic character of ordinal rank (Thomas and Bancroft), whereas Dr. Marie Stopes

has demonstrated that the same genus may have straight or sinuate walls to its epidermal cells in different species of fossil *Ginkgo* from the flora of the Inferior Oolite of Brora. Thus *Ginkgo digitata* had an epidermis, the walls of whose cells were sinuate, while *Ginkgo biloba* has cells whose epidermal walls are straight.

Detailed Account of New Leaves.

DICOTYLOPHYLLUM, nom. nov., for fossil dicotyledonous leaves of doubtful affinity.

DICOTYLOPHYLLUM STOPESII, sp. n. (Pl. 20. figs. 1-4). A single specimen was found by the writer in a clay boulder near the top of the West Cliff, about ten yards west of the West Cliff lift.

External Characters.—Simple, lanceolate tapering; apex somewhat blunt; coarsely serrate; teeth comparatively wide apart, from 7 mm. near the base to 4 mm. near the apex. Venation unicostate, lateral veins well marked. Length 5.6 cm.; width 1.6 cm.

Cuticular Structure.

Under Epidermis (Pl. 20. figs. 2, 3).—This consists of :—

(i.) *Thin-walled parenchyma*: Cells somewhat longer than broad, on the average .025 mm. by .018 mm. These parenchyma cells are also associated to form hair bases.

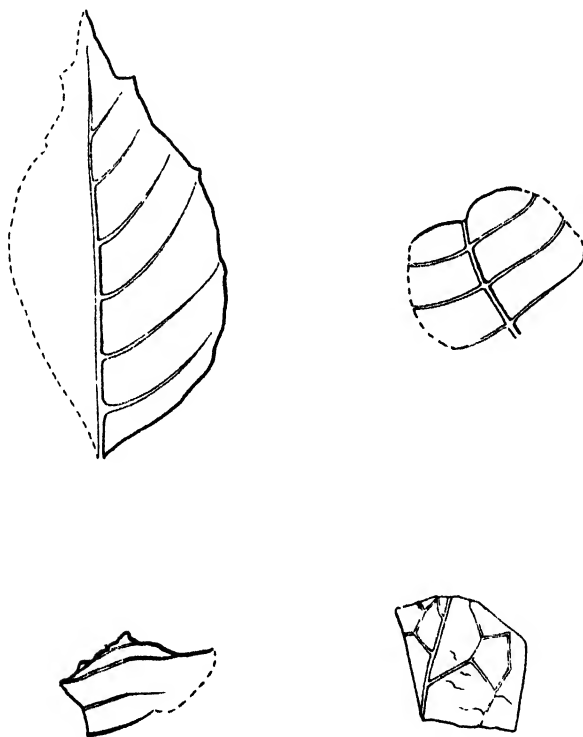
(ii.) *Guard cells of the stomata* associated with which are accessory epidermal cells varying in number from two to four or five. They bound open pores in the specimen examined. The stomata and guard cells are remarkably large. The average diameter of the latter parallel to the pore is .025 mm., and at right angles to the pore it is .025 mm., hence the stomata are isodiametric. They are very close together surrounding the bases of hairs which are frequently separated by a single row of stomata only, at the most by three rows. The hairs, or rather the hair bases, consist of radially grouped epidermal cells surrounding an opening; the walls are strongly thickened along the radii, especially towards the centre.

Upper Epidermis (Pl. 20. fig. 4).—The majority of the cells consist of ordinary epidermal parenchyma. There are numerous scattered hair bases, the average distance between which is .275 mm. The hair bases and the epidermal cells are similar to those described above. There are a few stomata, and thirteen or more epidermal cells intervene between them; their distance apart is very marked when compared with the close chain-like arrangement on the lower surface.

DICOTYLOPHYLLUM SPICULATUM, sp. n. (Pl. 20. figs. 5-9). One fairly complete specimen was found (see text-fig. 1), and many fragments in material communicated by Dr. Stopes. The leaf appears to have been extremely abundant, locally.

External Characters.—Simple, ovate (see text-fig. 1), acuminate, tip blunt. Just below the apex the leaf widened to form a narrow “shoulder” on each side. Margin finely sinuate, with more prominently bluntly dentate teeth at intervals of about 11 mm. between the flat finely sinuate sinuses. Unicostate; lateral veins paired, strongly marked, meeting the wide midrib at angle of 83° . Length 8.9 cm., greatest width 5.2 cm.

TEXT-FIG. 1.

*Dicotylophyllum spiculatum.*

Cuticular Structure.—Fragments of this cuticle were extremely common in very many of the different lumps of the Bournemouth material.

Under Epidermis (Pl. 20. figs. 5–8).—Under low powers of the microscope the unstained preparations show numerous roughly quadrangular grey patches, in the midst of each of which is a cruciform opening, the stoma. The quadrangular patches are parts of what are probably not guard cells but accessory cells which are packed with masses of structure apparently spicules, giving the appearance of heavy grey shading. The epidermal cells when examined with $\frac{1}{8}$ -inch objective are seen to be thick-walled, irregular in size, and very asymmetric. The accessory cells which surround the pore

are comparable in position with those of *Frenelopsis* (Thompson, 1912), and the guard cells are not visible. These accessory cells are very remarkably shaped. Each may be regarded as a crescent which in many cases has become pulled out at its greatest convexity to form a sharp angle, and again, instead of turning at each side of the crescent to form a smooth horn, forms a sharp angle with enormously thickened wall at the bend where the outer convex wall passes into the inner wall. Because of the acuteness of these angles, the junction of the two accessory cells forms a deep and wide sinus, bounding the pore. Owing to the projecting angle in the middle of each convex outer wall, their width at right angles to the pore is much greater than their diameter parallel to the pore, i. e., as .03 mm. is to .012 mm. They are filled with spicules, generally branched, which radiate fanwise from the inner to the outer walls, sometimes dividing into two groups in each cell, but sometimes being parallel to the long axis of the cell instead of at right angles to it. The writer does not believe these cell contents to be the result of post-mortem changes, although one must not exclude that possibility. The inner walls of the accessory cells are thick, appear corrugated, and bound a cruciform pore, two of the points of the cross following the projecting angle in the middle of each convexity of the cell, while the other two points of the cross are directed towards the lowest depression of the angular sinus at the junction of the accessory cells, as seen in surface view. Both stomata and accessory cells are remarkably asymmetric. Thus one cell may be distinctly smaller as a whole than its partner. Again, one cell of a pair may have one horn, usually a lateral horn, longer and more thickened than any other of the horns of the pair. The stomata occur between every one, two, or three epidermal cells. Veins of from seven to very many cells across, with some extremely thick-walled cells, and branching at a wide angle, intersect the surface. The cells which compose the vein are elongated and show some signs of sliding growth, some having one tapering and sharply pointed end, while the other end is blunt. Their thickness is not uniform. Numerous papillate cells with dome-shaped outer walls border the veins and lie upon them. They are at a higher level than the epidermal cells, require a different focus for their examination, and are thick-walled stone cells occurring in groups, forming mounds of cells whose outer walls appear dome-shaped. The individual cells are thick-walled and in many cases form rather irregular rosettes. The topmost cells are the smallest and have the thickest walls.

Upper Epidermis (Pl. 20. fig. 9).—This is sharply distinguished from the under epidermis by its lack of stomata. Its cells are thick-walled and consist of uniform parenchyma across which spreads a network of veins and papillæ similar to those of the under surface. The cells vary much in shape. They may be square or oblong or 5- or 6-sided with their edges frequently very rounded instead of being angular. One preparation showed very delicate

branched pits on the walls of some cells. The veins consist, as in the lower epidermis, of elongated cells with thicker walls, some tapering to a point at one end. Thus the whole epidermis of this leaf is extremely distinctive and can be recognised at a glance.

DICOTYLOPHYLLUM SINUATUM, sp. n. (Pl. 20. figs. 10–12). Three specimens of this leaf have been isolated. The first specimen α was found by the writer at Bournemouth, west of the pier; the second specimen β , V. 14917, a perfect leaf, and the third γ , V. 12645, not quite so complete, were identified, both from their external character and cuticular structure, from the Gardner Collection at the British Museum. Externally the leaves very much suggest the *Lauraceæ*.

Specimen α .

External Characters.—A fragment, evidently the basal half of an elliptical ovate leaf. Length 4·8 cm., hence the whole leaf was probably at least 9–10 cm. long. Greatest width, which was close to the upper end, 3·5 mm. Venation unicostate, midrib strongly marked. Lateral veins in opposite pairs, occasionally a lateral vein missing or obliterated by fossilization. These laterals were extremely delicate in contrast to the strongly marked midrib. Margin very slightly notched at intervals of about 1·5 cm.

Specimen β , V. 14917 (Pl. 20. fig. 10).

The measurements of the complete leaf were:—Greatest width 2·8 cm., length 12·4 cm.; length of stalk 1·6 cm.

The width of this specimen was less than that of Specimen α , hence α was probably longer than 14 cm. The midrib was strongly marked, the lateral veins were very faintly outlined, occurred apparently in pairs, and diverged from the midrib at an angle of about 40°. Each vein curved round just inside the margin and became connected with the vein above. The cuticle was histologically identical with that of Specimen α .

Cuticular Structure.—*Under Epidermis* (Pl. 20, figs. 11 & 12). Epidermal cells irregular in shape and very sinuate, with ten or eleven crests and troughs. They are so asymmetric that some are almost triangular, others square, while yet others are elongated in one direction but with two sides parallel forming sinuate oblongs. *Stomatal apparatus* consists of pairs of guard cells and pairs of subsidiary cells. The stomata vary much in size owing to marked differences in the size of different pairs of guard cells and marked differences in the diameter of different pore-spaces. The junction of the two crescent-shaped cells is extremely thick-walled, the thickening tapering to a point towards the pore giving the appearance of a dagger. There is also a thickened ridge at right angles to the “dagger,” the whole thickening thus forming a “T” piece, the cross-bar of the T fitting into a depression between the horns of the two crescents so that a pair of daggers

occurs between the two guard cells. Some of the guard cells, but not all, are widest at right angles to their length.

Average width of guard cells across the pore $\cdot 022$ mm.

Average width of guard cells parallel to pore $\cdot 026$ mm.

A very narrow, deeply staining subsidiary cell with granular contents forms a border round the outer edge of each guard cell, and while the latter become yellowish with saffranin, the former stain very deeply pink. The average width of the subsidiary cells is $\cdot 004$ mm.

Veins: These consist also of cells with sinuate walls, but they are elongate, narrow, and less deeply sinuate than the ordinary epidermis. They are about 7 cells wide. Average length of a cell $\cdot 03$ mm., average width $\cdot 009$ mm. *Hairs or papillæ bases*: These are like raised spiked collars and of very definite appearance, resembling in shape the spiked collars which formed mediæval instruments of torture. These hair bases are very thick-walled with six or more radiating, sometimes bifurcate spikes of thickening, which gradually thin out peripherally and become continuous with the walls of adjacent cells. The "collar" itself would seem to be a single cell with a very thick and spiky wall and raised above the level of the cells around.

Upper Epidermis consists of epidermal cells with sinuate walls, and more approximately rectangular than those of the lower epidermis. Veins of similar cells but narrower and longer occur also.

ARAUCARITES GÖPPERTI (Sternberg) Gardner. (Pl. 20. figs. 13, 14.)

This was first found in the form of separate curved polished brown and black isolated teeth and minute twig fragments, when clay lumps of material from the West Cliff and from Durley Chine were washed in the search for leaves, etc. Comparison with figures of cuticular preparations by R. Florin (1919) suggested a strong resemblance to *Sequoia*, with which leaf the tooth-like appearance was in agreement. Specimens in the Gardner Collection were also examined, and their cuticular structure was found to be identical. A specimen figured in Gardner's 'Eocene Flora' as *Araucarites Göpperti* (vol. ii. p. 104, pl. 12. fig. 1) was also compared, and chemical treatment of its cuticle revealed its identical nature.

External characters of a Leaflet.—Each leaflet is 6–10 mm. long, strongly curved or sickle-shaped, quadrangular in cross section, and decurrent with the stem at the base where the leaf is 2 mm. wide, tapering to 1 mm. and less towards the acute apex. These leaflets are spirally arranged.

Cuticular Structure.—The stomata occur in two bands parallel to the long axis of the leaf; widen out and are more irregular towards the base. Each band consists of two or three long rows of stomata irregularly grouped into

twos and threes alternate with each other. Near the extreme apex one linear series of stomata forms the band. The orientation of the stomatal axes is extremely variable—parallel to, at right angles to, and oblique to the long axis of the leaf. The stomata show, however, a most characteristic arrangement of cells. The space occupied by the two guard cells is quadrilateral to oval in outline, or occasionally round. The guard cells themselves are somewhat ill-defined, partly because they appear to be only weakly cuticularised, partly because they become readily destroyed by the chemical treatment they undergo. Moreover, they lose clearness because they are below the level of the epidermal cells. The guard cells are surrounded by four or occasionally five narrow elongated cells placed end to end forming a ring. These accessory cells stain very deeply with methyl green or safranin. The inner wall of each subsidiary cell where it bounds the guard cells is strongly thickened, as are the radial walls also. The stomata occur on both surfaces of the leaf.

Epidermal Cells.—One or two rows of epidermal cells occur between the two or three rows of stomata in a band. The epidermal cells occurring between two stomata in one linear series are elongated in the horizontal direction, *i. e.*, at right angles to the long axis of the leaf, while between two parallel rows of stomata they are elongated more or less parallel to the long axis of the leaf. They are thick-walled, and contain numerous large, simple round pits which show especially well in the stained sections. The walls are straight, not wavy. The *midrib* consists of 13–20 rows of narrow vertically elongated cells, as one passes from apex to base of the leaf.

Measurement of Cells :—

	<i>Stomata.</i>	<i>Subsidiary Cells.</i>
Average length	·03 mm.	·024 mm.
Average width	·0175 mm.	·012 mm.

Epidermal Cells.

	Between two stomata of a series.	Between the series of stomata.
Average length	·025 mm.	·042 mm.
Average width	·012 mm.	·01 mm.

Discussion as to the Affinities of Araucarites Göpperti.

Gardner believed the leaf to be a true *Araucaria*. The species was founded originally on sterile branches from the Eocene Flora of Haering in the Tyrol, which were considered to be externally identical with foliage shoots of *Araucaria excelsa*, but Ettingshausen recorded it from Bilin in Bohemia under the generic name of *Sequoia*, and the question now arises as to whether the leaf is an *Araucaria* or a *Sequoia*. In order to see whether the cuticular

structure would reveal the generic character, preparations have been made of various recent and fossil *Sequoias* and recent *Araucarias*. Gardner believed it to be closely related to *Araucaria Cunninghamii*, and externally it is extraordinarily like the latter species. The cuticular structure, however, does not support this view.

Let us now consider the structure of some recent *Araucarias* :—

<i>Araucaria Cunninghamii</i> .	<i>Araucaria excelsa</i> .	<i>Araucaria Bidwillii</i> .	<i>Araucaria imbricata</i> .
Average length of leaflet, 8-10 mm.	Leaflets of two different habits, 7-8 mm. in length, in compressed form, while in spreading form length is 10-15 mm.	4 cm.	5 cm.
Average width of leaflet, 2 mm. at base.	1-2 mm. in each case.	1 cm.	2.8 cm.
Arrangement—Spiral.	Spiral, laterally compressed, imbricate, or spiral spreading at right angles to the stem, slightly decurrent.	Spiral, spreading, slightly decurrent at the base.	Spiral, spreading.
Shape—Falcate.	Falcate.	Ovate-lanceolate.	Ovate.

The external characters of *Araucaria Bidwillii* are not in agreement with those of *Araucarites Göpperti*.

The falcate, laterally compressed imbricated short-leaved form of *Araucaria excelsa* is extremely like *Araucaria Cunninghamii*, and also like the fossil form, but the latter shows marked decurrence.

Cuticular Structure of Araucaria Cunninghamii (Pl. 20. figs. 15, 16).

The stomata occur in bands on both surfaces. Each band consists of three or four linear series more regularly grouped than those of *Araucarites Göpperti*. The stomata are closely packed, and in many cases no epidermal cells intervene between them. The stomatal axes are extremely variable in direction. Four or five, but more commonly four, subsidiary cells surround the guard cells, have thick radial and outer walls, and stain deeply. The epidermal cells have very wavy walls and are very thick-walled, showing pits: thus it would seem that if *Araucarites Göpperti* is an *Araucaria*, it must be a different species of *Araucaria* from *Araucaria Cunninghamii*, since the walls of its epidermal cells are straight. Dr. Marie Stopes has shown (Stopes, 1907) that in the case of the recent and fossil Ginkgos, wavy or straight epidermal walls must be regarded as a specific character, though externally no difference could be detected between the recent and fossil forms.

Cuticular Structure of Araucaria excelsa (Pl. 20. figs. 17, 18).

Stomata.—These are situated on the floor of fairly large pits, occurring both on upper and lower epidermis, and in bands parallel to the long axis of the leaf. A band consists of widening linear rows of stomata, two rows near the extreme apex, the number of the rows rapidly increasing from apex to base so that near the base there are five linear rows of stomata in a band. There are from 30–38 rows of epidermal cells in the middle of the leaf between the two stomatal bands of the leaf. In the fossil specimen, although the band of stomata widens slightly near the base, more than three linear series of stomata in a band have not been found, while at the extreme apex, one linear series only occurs. The guard cells of the stomata of *A. excelsa* are surrounded by four, more rarely five, subsidiary epidermal cells which occur above them, and have slightly thickened inner walls and somewhat more thickened radial walls. The opening of the pore can be seen as a narrow, sharply angled slit, and the granular guard cells can also be seen. The subsidiary cell group is larger than in the fossil specimen.

Epidermal Cells.—Two to three rows of epidermal cells occur between each linear series of stomata in a band; in places one row only occurs, owing to the somewhat irregular grouping of the stomatal lines. In the fossil there is commonly a single linear series of epidermal cells between two adjacent lines of stomata in a band. Occasionally two or three rows of epidermal cells occur, especially passing towards the base of the leaf. In *Araucaria excelsa* the epidermal cells between the rows of stomata are elongated parallel to the long axis of the leaf, but between the stomata in a row they are somewhat elongated horizontally. The epidermal cells when seen with a low power appear to be straight oblong rectangles, but under a high power show distinct sinuations here and there. Thus one wall of a cell may be sinuate, the others almost straight, and this wavy wall may be a vertical or a cross wall. There may be a few sinuations only in the wall or they may be numerous. One cell showed one wall with five sinuses and another with three. One marked sinus in the cross wall is fairly common. Actual preparations show this better than the photographs do, for the sinuations in the photomicrographs are somewhat blurred. Simple pits seen on edge are very common and occur at the bases of the sinuses, which are, when present, much less deep than those of *Araucaria Cunninghamii*. The sinuations are narrow and shallow, and occur rather locally, and large parts of a field may show none.

Cuticular Structure of Araucaria Bidwillii (Pl. 20. fig. 19, Pl. 21. fig. 20).

Here the upper surface is practically destitute of stomata. The under surface bears linear series and the uniseriate rows are not grouped into bands. Two, three, or four epidermal cells intervene in linear series between adjacent stomata in a vertical row, and these are *elongated* in the *vertical*

direction, in marked contrast with the corresponding cells of *A. excelsa*, *A. Cunninghamii*, and *A. Göpperti*. The cells between two stomata of a series are markedly wider and shorter than those between two rows of stomata, though elongated in the same direction parallel to the long axis of the leaf. The number of vertical rows of epidermal cells between two linear series of stomata is variable, being from four to fourteen.

Stomatal Apparatus.—The stomata are situated on the floor of pits roofed in by four or five or more somewhat irregularly grouped subsidiary epidermal cells. These disturb the symmetrical arrangement of the parallel rows of epidermal cells between the stomatal lines, and cause the epidermal cells in their neighbourhood to curve round them, the appearance presented by a stomatal line being that of a row of large beads on a thin string—each bead being a group of subsidiary cells, and the string, the connecting epidermal cells of the same linear row. The poral opening is a narrow oblong with bluntly rounded ends, between which the granular guard cells can be seen. The stomatal axes are not oblique. The long axis of each is parallel to the long axis of the leaf. The subsidiary epidermal cells are not all alike. Two, those parallel to the long axis of the pore, are elongated vertically and short horizontally. The two which close in the pore horizontally are not much longer in one direction than the other. It is evident that neither external form nor cuticular structure suggest a very close relationship between *A. Bidwillii* and *A. Göpperti*.

Cuticular Structure of Araucaria imbricata (Pl. 21. figs. 21, 22).

Stomata occur on both surfaces of the lamina, and are, as in the other species of *Araucaria*, situated on the floor of pits. The epidermis is extremely thick-walled. Stomata occur in very regular linear series, each series being separated from the next by three to seven rows of thick-walled cells. Each series is uniseriate, and the stomata are very close, a line of eleven stomata having no interspersed epidermal cells, and then the series is interrupted by two epidermal cells separating the eleven from another five stomata, these succeeded vertically by two epidermal cells and then nine stomatal cells, and so on.

Stomatal Apparatus.—The subsidiary cell group is larger in all directions than the corresponding group of cells in *A. Göpperti*, and larger in all directions than the ring of cells surrounding the pore in *A. Bidwillii*. It is very considerably larger than the equivalent cell group in *A. excelsa*. The poral axes are not absolutely parallel to the length of the leaf, but are slightly oblique, though much less so than in *A. excelsa* and *A. Göpperti*. The oblong pore is very thick-walled, elongated, and narrow; through it, in some cases, the slightly open guard cells can be seen.

Thus, when we compare the external characters and the relative diameters of the axes of the poral ring, and of the epidermal cells of the

various *Araucarias*, it is evident that there are, in many respects, points of agreement between *Araucaria excelsa* and *Araucarites Göpperti*, but fewer and fewer points of agreement between *A. Göpperti* and *A. Cunninghamii*, *A. Bidwillii*, and *A. imbricata*.

	<i>Araucarites Göpperti</i> .	<i>A. excelsa</i> .	<i>A. Cunninghamii</i> .	<i>A. Bidwillii</i> .	<i>A. imbricata</i> .
Stomatal pore.	Long axis .03 mm. Short „ .0175 mm.	.033 mm. .014 mm.	.035 mm. .014 mm.	.038 mm. .01 mm.	.039 mm. .015 mm.
Subsidiary epidermal cells.	Long „ .024 mm.	.04 mm.	.038 mm.	Vertical cells. .052 mm.	Horizontal cells. .022 mm.
	Short „ .012 mm.	.02 mm.	.02 mm.	.03 mm.	.016 mm.
Epidermal cells between two stomatal series.	Long „ .04 mm.	.058 mm.	.058 mm.	.11 mm.	.076 mm.
	Short „ .015 mm.	.01 mm.	.019 mm.	.012 mm.	.029 mm.
Epidermal cells between two stomata of one series.	Long „ .025 mm.	.026 mm.	.034 mm.045 mm.
	Short „ .012 mm.	.016 mm.	.032 mm.019 mm.

Recent and extinct *Araucarias* have been described by Seward & Ford (1906) very fully, but no details of their epidermal structure other than the presence or absence of stomata on the two surfaces are dealt with in their paper. It is very evident that all the *Araucarias* conform as regards their stomata to a well-defined morphological type, in which the stomata are serial and individually separate, and occur at the bottom of epidermal pits formed by the dipping down of the subsidiary cells surrounding the guard cells. The *Araucarian* leaf-epidermis shows much in common with that of a *Sequoia*, as does also the fossil specimen *A. Göpperti*, and some *Sequoia* leaves will now be described in order to ascertain whether their cuticular structure shows more points of resemblance with *Araucarites Göpperti* than do the *Araucarian* cuticles.

SEQUOIA GIGANTEA, Lindl. & Gord.

External characters of a leaf on a sterile shoot.—Length 5–8 mm., cross section triangular to rhombic. Average width 1 mm. Arrangement spiral and decussate, adpressed but with free tips. Leaves occurring on the shoots bearing cones are shorter, broader, and overlap more.

Cuticular Structure of Sequoia gigantea (Pl. 21. figs. 23–25).—This has been described by Rudolph Florin (1920). He does not give detailed measurements of the size of the various cells, but merely the ratio between their length and breadth in each case. He describes the stomata as occurring on both surfaces of the leaf, and says that the space between the rows of stomata varies just as does the distance between each row. He says further, that they are orientated lengthwise and that their long axis is also parallel to the direction of the vascular bundle, and points out that the openings do not lie in definite parallel closely connected rows any more than do the cells surrounding them, but between the rows of stomata, on the contrary, the epidermal cells lie in fairly regular vertical rows, and have an elongated form. The ratio of breadth to length varies from 1 : 10 to 1 : 4. The opening between the epidermal cells which surround the guard cells is 11μ broad and 31μ long.

Detailed characters of the Cuticle (Pl. 21. figs. 23, 24, 25).

I find there is a distinctly banded arrangement of the stomata, two bands occurring on either side of the wide midrib, these are somewhat irregular, and the number of serial rows making up a band varies from two to five according to the distance from the apex. At the extreme apex a band consists of a single linear series of stomata, while at the base the banded arrangement is difficult to recognise owing to the widening out of all the series and the increase in the number of rows comprising the band. The stomatal axes do not preserve an exact parallelism, and though many are vertically orientated, a considerable number are oblique to horizontal in direction. This is comparable with the orientation of the stomatal axes in *Araucarites Göpperti*, but there is relatively greater axial obliquity in the stomata of *Araucarites Göpperti*. The middle of the leaf is occupied by a wider zone of vertically elongated narrow cells with rather oblique cross-walls. On either side of this zone and between the stomatal series the parenchyma is less regular, and the cells are shorter and wider, and though some are still vertically elongated, others have their long axis horizontal. The pore is an oblong slit surrounded by a ring of five, occasionally four or six, epidermal cells. Through the pore formed by this ring, the guard cells can be seen. Each stomatal series consists of a varying number of epidermal cells, two to five or many intervening between successive stomata, which are usually not in very parallel lines. One, two, or three rows of epidermal cells intervene between each series, the number increasing towards the base.

The average length of the poral opening is .022 mm.

The average width of the poral opening is .009 mm.

Hence ratio of length to width is 2 : 1.

The subsidiary epidermal cells have an average length of .0309 mm., and an average width of .019 mm.

Hence ratio of length to breadth is 2 : 1.

The *epidermal cells* between two stomata of a series have an *average length* of $\cdot 032$ mm. and an *average width* of $\cdot 019$ mm.

Thus the ratio of length to width is 2 : 1.

The *epidermal cells* between two linear series of stomata have an *average length* of $\cdot 064$ mm. and an *average width* of $\cdot 019$ mm.

Hence ratio of length to width is 3 : 1.

SEQUOIA SEMPERVIRENS, Endl.

External Characters.—The general appearance is very different from that of *Sequoia gigantea* or the fossil *Araucarites Göpperti*. The narrow oblong leaves spread outwards from the stem at an angle of 45° . The midrib is prolonged to form a short spine-like tip. Average length 1·8 cm. ; average width 2 mm.

This leaf has also been described by Rudolph Florin.

Cuticular Structure (Pl. 21. figs. 26, 27).—Stomata occur on both upper and under surfaces, and are arranged in linear series which are grouped to form a wide band on either side of the midrib on the under surface, but the stomata are very few on the upper surface, three rows of widely separated stomata alone being found, and in one preparation only, while other preparations showed no stomata on the upper surface.

Stomatal Apparatus.—The poral ring of subsidiary cells consists of commonly four, less frequently five cells, and of these, those orientated vertically are much longer than those which close in the ring horizontally. The horizontally disposed cells serve in some cases as connecting cells between one stomatal pore and the next, and then are vertically or in some cases obliquely elongated. The vertical cells have one end produced in some stomata, beyond the other cells, forming horn-like projections. The long axes of the openings are vertical to oblique.

Epidermal Cells.—The series of stomatal lines and epidermal cell rows are all curiously waved. This is due to the ring-like group of poral cells being large and causing the epidermal cells of either adjacent vertical line to curve round them. This wavy outline makes the cells difficult to measure. The cells, both between the individual stomata and between adjacent stomatal series, are mainly vertically elongated, though the cell next to one of the poral ring and in a vertical line with it is sometimes longer horizontally. The cross walls of the cells are oblique and somewhat curved, not very angular. The cells between two different stomata of a series are much shorter and wider than those between two different stomatal series. The ratio of length to width is 2 : 1 in the former case and 7 : 1 in the latter case. The *midrib* is about 17 cells wide. Its cells are extremely long and narrow, with very oblique end walls ; ratio of length to width is 10 : 1.

Upper Epidermis.—The whole preparation showed nine stomata in three wide apart serial rows. The *poral rings* are smaller than those of the lower

surface. This is due partly to the smaller size of the individual cells of the ring, and partly to the smaller size of the pores. The *epidermal cells* are distinctly shorter than those of the lower epidermis.

Average diameter of short axis = .022 mm.

Average diameter of long axis = .269 mm.

Kräusel (1920, p. 353) considers that the cuticular structure of *S. sempervirens* is very much like that of *Sequoia Langsdorffii*, and like the figures which Reid gives of *S. Couttsiae*, but he does not seem to have examined Reid's material.

SEQUOIA TOURNALII, Brongn. Gardner has described this from the Myrica Bed of the Middle Bagshot of Bournemouth, and states that although there is no direct evidence to connect it with any particular tribe of Conifers, it more nearly resembles *Sequoia sempervirens* than any other species. It is also very similar to *Sequoia Langsdorffii*.

The following account is based on specimen V. 15103 (Brit. Mus., N.H.), the external form of which is figured in Gardner's 'Eocene Flora,' plate 5, fig. 12.

External Characters.—Average length 1.6 cm.; average width 2.25 mm. The foliage on one and the same branch may be imbricated and decurrent and much like that of *Sequoia gigantea*, or distichous and decurrent, much longer and wider and externally extremely like the foliage of *Sequoia sempervirens*. This is interesting in view of the fact that Miss Eastwood (1895) finds two different types of foliage on trees of *Sequoia sempervirens*: "All large trees of *Sequoia sempervirens* have the upper foliage quite different from the lower, with intermediate forms."

Cuticle (Pl. 21. figs. 28, 29, 30).—Both upper and under surface bear stomata in vertically elongated serial rows; the pores are close together, separated by only one or two epidermal cells, while each vertical row of stomata is similarly separated from the next by one or two epidermal cells. Epidermal cells and pores are constructed on a much smaller scale than those of any of the known Sequoias examined, nor is there the sharp distinction between ring cells surrounding the pore and the remaining epidermal cells that is so characteristic of the Sequoias. The pores are all orientated vertically, the opening is a narrow oblong, its long axis vertically directed. The midrib is about 18 cells wide, and some of its cells, which are much shorter than those of the midribs of known Sequoias, have slightly sinuate walls.

Stomatal Pores.—The guard cells cannot be seen, but the pore shows as an opening bordered by four epidermal cells, two closing it in laterally, and these appear to be those of the adjacent epidermal cell rows, slightly distended, while the two which close in the pore horizontally are also vertically elongated and form continuations of the epidermal cells in the same linear series. Very occasionally a short, almost isodiametric cell is cut off to close in the pore horizontally.

Epidermal Cells.—These are relatively much shorter and wider than those of known *Sequoias*, with ends oblique to flat, round rather than angular, and many show sliding growth. There is no marked difference between those alternating with the serial rows of stomata and those between individual stomata, but there is a marked difference between these and those of the midrib.

Thus, when we compare this leaf with that of *Sequoia sempervirens*, we see that while the external characters are in agreement, the cuticular structure is not sufficiently alike in the two leaves for the specimen to be identical specifically with *S. sempervirens*. The construction of the pore occasionally presents considerable resemblance in the two cases. Thus what is of common occurrence in *Sequoia Tournalii*, namely the vertically elongated horizontal cell closing in the pore and serving as a connecting cell between one pore and the next in the same linear series, may also be seen in *Sequoia sempervirens*, but as the exception rather than the rule. *Sequoia sempervirens* usually has a short connecting cell cut out horizontally. In *Sequoia Tournalii* too, the stomatal series and epidermal cell rows present the same waved appearance owing to the divergence from the vertical of each linear series. A very short cell may close in the poral ring in *S. Tournalii*, as is commonly seen in *Sequoia sempervirens*. The vertical cells of the poral ring may have an end produced beyond the other cells of the ring in *S. Tournalii*, just as commonly occurs in *Sequoia sempervirens*, but in *S. Tournalii* the prolongation of the cell is not so marked. The chief points of difference are differences of size of all the cells, and the absolutely vertical orientation of the stomatal pores in *Sequoia Tournalii*, while the stomata in the fossil species do not show so clearly the banded arrangement characteristic of the living form, but seem evenly distributed right across the leaf in serial rows, except along the midrib. The shape of the epidermal cells is very similar, and the end walls are much alike in the fossil and recent species, if we allow for the far greater relative length in *S. sempervirens*.

SEQUOIA COUTTSIEÆ, Heer. Scales and seeds of this species as well as its sterile shoots have been found in the lignite of Bovey Tracey, which is regarded as of Oligocene age, and the cuticle has also been figured by Reid (1910). This fossil *Sequoia* is more delicate in appearance than either *Sequoia gigantea* or the fossil *Araucarites Göpperti* which so much resembles *Sequoia gigantea*. The stem is relatively thicker and the leaves wider apart, narrower and more sharply pointed, but also decurrent. The space between two leaves in a vertical series is 2 mm.

Cuticle (Pl. 21. figs. 31, 32).—Here, as in the other two species of *Sequoia*, i. e. *S. gigantea* and *S. sempervirens*, the stomata form bands. The stomatal pores are roughly four-sided and surrounded by an oblong ring of four or five narrow elongated cells. Epidermal cells between the stomatal rows are vertically elongated parallel to the direction of the midrib, which consists of about 15–30 rows of cells. The epidermal cells between two stomata in the

same vertical series are square or elongated horizontally, or less frequently vertically. Outside the stomatal bands, the epidermal cells are irregular both in shape and direction, and relatively wider in proportion to their length than those between the linear stomatal series.

Stomatal Apparatus.—Stomata occur on both surfaces of the leaf. The stomatal bands are extremely irregular, and by no means follow accurate vertical lines, a band consisting of about four series of divergent stomata which widen out and increase to about 7 or 10 rows towards the base of the leaf. The poral axes vary greatly in direction, being oblique or horizontal to vertical.

Although there are only two recent species of the genus, it was represented by numerous fossil species in Tertiary times, both on the Continent of Europe and in America. These species were based largely on foliage impressions, and probably a large proportion were inaccurately named. One anatomically known species from this country, *Sequoia giganteoides*, Stopes, occurs in Southern England in Lower Greensand rocks (Stopes, 1915). Thus the Sequoias have a long fossil history. *Sequoia Tournalii* is an older fossil than *Sequoia Couttsiae*, and there are therefore now three Sequoias from British rocks which are anatomically known, the cuticular structure of *Sequoia Tournalii* being here described for the first time. The systematic position of *Sequoia Tournalii* is, however, not nearly so well established as that of *Sequoia Couttsiae*, and while its external characters are in close agreement with those of *Sequoia sempervirens*, it must be borne in mind that the external characters of many living genera are very confusing and difficult to sort out. The cuticle of this fossil form seems to conform to the gymnospermous plan, but its points of contact with undoubted Sequoias are not very numerous, and whether it is a *Sequoia* must be considered not proven until specimens with cones are definitely identified.

The following table gives comparative measurements of the known Sequoias with *S. Tournalii* and *Araucarites Göpperti*.

<i>Sequoia gigantea.</i>	<i>Sequoia Couttsiae.</i>	<i>Sequoia sempervirens.</i>	<i>Sequoia Tournalii.</i>	<i>Araucarites Göpperti.</i>
Length 5 mm.	4 mm.	1·8 cm.	1·6 cm.	6–10 mm.
<i>Leaf.</i>				
Width 1 mm.	6 mm.	2 mm.	2·25 mm.	2 mm
<i>Cuticle:—</i>				
<i>Stomata.</i>				
Banded arrangement. Occur on both surfaces.	Irregularly banded arrangement. Occur on both surfaces.	Banded arrangement. Mainly on under surface.	Banded arrangement not clearly defined. Stomata appear to occur on both surfaces.	Banded arrangement well marked. Stomatal bands occur on both surfaces.

<i>Sequoia gigantea.</i>	<i>Sequoia Coultatae.</i>	<i>Sequoia sempervirens.</i>	<i>Sequoia Tournalii.</i>	<i>Araucarites Göpperti.</i>
<i>Poral Axes.</i> Vary in direction. Frequently oblique.	Vary in direction.	Long axis orientated vertically usually, occasionally oblique	Long axis vertically orientated.	Vary in direction. Usually oblique.
<i>Diameters of Pore.</i> Long axis ·022 mm. Short axis ·099 mm.	·024 mm. ·015 mm.	·037 mm. ·015 mm.	·013 mm. ·005 mm.	·03 mm. ·017 mm.
<i>Cells of the Poral Ring.</i> All similar. Long axis ·0309 mm. Short axis ·019 mm.	All similar. ·027 mm. ·008 mm.	Differentiated into two sets. <i>Vertical Cells.</i> ·062 mm. ·017 mm. <i>Horizontal Cells.</i> ·032 mm. ·025 mm.	Differentiated into two sets. <i>Vertical Cells.</i> ·031 mm. ·012 mm. <i>Horizontal Cells.</i> ·03 mm. ·039 mm.	All similar. Long axis ·024 mm. Short axis ·012 mm.
<i>Epidermal Cells of the Midrib.</i> Long axis ·074 mm. Short axis ·014 mm.	·041 mm. ·012 mm.	·27 mm. ·024 mm.	·071 mm. ·017 mm.	·037 mm. ·013 mm.
<i>Epidermal Cells.</i> <i>Between two stomatal series.</i> Long axis ·064 mm. Short axis ·019 mm.	·031 mm. ·016 mm.	·096 mm. ·013 mm.	·043 mm. ·014 mm.	·042 mm. ·010 mm.
<i>Between adjacent stomata of same series.</i> Long axis ·032 mm. Short axis ·019 mm.	·024 mm. ·017 mm.	·049 mm. ·028 mm.	·043 mm. ·014 mm.	·025 mm. ·016 mm.

There are very close points of resemblance between *Sequoia gigantea*, *Araucarites Göpperti*, and *Araucaria excelsa*. The following table will show how close the resemblances are :—

<i>Sequoia gigantea.</i>	<i>Araucarites Göpperti.</i>	<i>A. excelsa.</i>
<i>Leaf.</i> Length 5-8 mm. Width 1 mm.	6-10 mm. 2 mm.	6-15 mm. 1-2 mm.
<i>Cuticle:— Poral Axes.</i> Long axis .022 mm. Short „ .009 mm.	.03 mm. .017 mm.	.033 mm. .014 mm.
<i>Cells of the Poral Ring.</i> Long axis .031 mm. Short „ .019 mm.	.024 mm. .012 mm.	.04 mm. .02 mm.
<i>Epidermal Cells between two stomatal series.</i> Long axis .064 mm. Short „ .019 mm.	.042 mm. .010 mm.	.058 mm. .010 mm.
<i>Epidermal Cells between two adjacent stomata in the same series.</i> Long axis .032 mm. Short „ .019 mm.	.025 mm. .012 mm.	.026 mm. .016 mm.

The poral ring cells are distinctly larger in *Araucaria excelsa* than in *Araucarites Göpperti*, whose measurements in this respect agree more closely with those of *Sequoia gigantea*, but when the sum total of the various measurements of these three leaves is estimated, it seems to point to the Araucarian relationship of *A. Göpperti*.

TAXODIUM EUROPAEUM (Brongn.).

Its external characters have been figured by Gardner (1883, pl. 3. fig. 3). Specimen V. 15072 was examined by the writer for anatomical investigation, in the hope of obtaining confirmatory evidence of its true generic character, since none of the Bournemouth fossils so-named possess cones, though the material named *Taxodium europæum* by Brongniart from Tertiary beds in Greece possessed cones.

External Characters.—These have been described by Gardner. Leaves imbricated, closely adpressed, decurrent, and alternate in arrangement, small, and acute or obtuse. Scale-like and triangular forms occur near the base of the shoots, while near the shoot-tips they are a little longer, awl-shaped and recurved. Average length 2.2 mm. Average width .57 mm. The recurved character of the leaves is comparable with that of *Glyptostrobus*.

Cuticular Structure (Pl. 21. fig. 33, Pl. 20. fig. 34).

Stomatal Apparatus.—The stomata show a banded arrangement, and appear to occur on both sides of the tiny leaf. One band appears to consist of four or five rows situated in epidermal pits. The poral axes appear as a whole to be orientated lengthwise, but their orientation may be oblique or transverse. The pores are usually bounded by four epidermal cells, but five epidermal cells surrounding the pore are not uncommon, forming a rosette. When four cells surround the pit, two are orientated transversely, and two parallel to the direction of the poral axis. One of the transverse cells may be much drawn out and longer than the others. This is also seen in the modern *Glyptostrobus* cuticle. The elongated cell may join the next poral ring obliquely.

Epidermal Cells elongated parallel to the long axis of the leaf. One end of a cell may be much narrower than the other, owing to the obliquity of some of the cross walls. The cross wall may be curved instead of plane. One, two, or three rows of epidermal cells intervene between the linear series of stomata. A few of the longitudinal walls of the epidermal cells show slight sinuations. The epidermal cells intervening between two linear series of stomata are somewhat narrower than those in the middle of the leaf. One epidermal cell only may separate one pore from the next, of the same or an adjacent linear stomatal series, since the stomata may occur very close together in a band.

Average length of an epidermal cell between two linear series, .039 mm.

Average width of an epidermal cell between two linear series, .017 mm.

Discussion as to the Affinities of Taxodium europæum.

It has been suggested that possibly *Taxodium europæum* is a polymorphic form of *Sequoia*. The cuticular structure is, however, distinctive, and does not bear out this view. In order to compare it with recent forms, preparations of *Taxodium distichum* and of *Glyptostrobus heterophyllus* have been made, and the cuticular structure of these species will now be described. Externally, *Taxodium europæum* exhibits more likeness to *Glyptostrobus heterophyllus* than to *Taxodium distichum*, but, as we have seen, external resemblances may be fallacious, and considered alone are frequently valueless. The cuticles of the three leaves will therefore now be compared before any deductions are made. Kräusel, 1919, p. 110, describes *Taxodium europæum* as *Glyptostrobus europæus*, and considers it externally much like *Widdringtonia helvetica*, but cones were not found.

TAXODIUM DISTICHUM, Rich.

External Characters.—Leaves deciduous, distichous, acute, green, not scale-like, standing out from the stem at an angle of about 45°.

Cuticular Structure (Pl. 21. figs. 35, 36).

Stomatal Apparatus.—Florin (1920) has described the cuticle. He says that the lower surface always bears two bands of stomata, each band consisting of five rows, and that the upper surface often bears several rows of stomata on each side of the midrib. He quotes Mahlert (1885) as describing the stomata lying in longitudinal rows on the under surface of the leaf, parallel to the orientation of the vascular bundles, but with the long axis of the pore, in the majority of instances, placed at right angles to the long axis of the leaf. Mahlert describes the stomata of the upper surface of the leaf as being without definite orientation on either side of the middle line. Florin finds that the stomata on the under surface, as also on the upper surface, are not always transversely placed, but show much axial variation, every transition between the transverse and longitudinal direction of the long axis of the pore being seen, although the greater number of stomata show more or less clearly that the long axis of the pore is placed at right angles to the length of the leaf. The stomata, he says, are usually surrounded by four epidermal cells, of which two are often halfmoon-shaped and orientated in the longitudinal direction. The poral diameters he gives as about 26μ in length and 14μ in breadth. I find in my preparations that the arrangement he describes is very common, but I also find, not infrequently, pores surrounded by FIVE EPIDERMAL cells forming a rosette arrangement (see fig. 35). This is a point of interest, as it is also seen in *Taxodium europæum* and, moreover, there is extreme variability in the size and orientation of the cells surrounding the pore. They are much less definitely specialised than are those of *Glyptostrobus* or *Taxodium europæum*.

Epidermal Cells.—Florin describes the epidermal cells also. He says that a varying number, of different sizes, intervene between the individual stomata in a row, while between the rows of stomata usually a single series intervenes, and further, that the cells are rectangular, orientated in the longitudinal direction, and not strongly thickened. The ratio of breadth to length he gives as 3 : 20–3 : 10.

I find that, while this is the general plan, close examination shows that there is some variation. Thus two rows of cells may intervene between the stomata, as occurs also in *Taxodium europæum*. Some of the epidermal cells are slightly oblique in their orientation, others are transversely placed and the rows are not strictly parallel, but tend to run into each other. Some of these cells again are narrower at one end than at the other, just as in the fossil form. Kräusel (1920) has described a fossil form, *Taxodium distichum miocenicum*, from the Tertiary flora of Silesia. It is considered much to resemble *Sequoia Langsdorffii*, but to differ from it in the absence of a decurrent base.

GLYPTOSTROBUS HETEROPHYLLUS, Endl.

The recent material of this leaf was supplied from the herbarium in the Botanical Department of the British Museum (Hb. Hance, 5276).

External Characters.—Leaves persistent, and rather variable in form, similar in habit to those of *Taxodium*, but not two-ranked, spiral, closely packed, decurrent, and somewhat falcate, with the arch of the sickle bending outward, not inward, as in *Sequoia* and *Araucarites*. The tip is narrowed and acute.

Cuticular Structure (Pl. 21. figs. 37, 38).

Stomatal Apparatus.—The stomata show a banded structure and occur on both sides. A band consists of about four irregular rows of stomata, which are sunk beneath large pits. The poral axes are very variable in direction, but many are orientated parallel to the long axis of the leaf. The pores are bounded by four, five, or six deeply staining cells, but five is the commonest number. The arrangement of the encircling cells is variable. When four surround the pore, they do not show the definite grouping Florin describes for *T. distichum*, i. e., two disposed longitudinally and semilunar in shape, and two disposed transversely. Frequently two occur on each side, the junction in the longitudinal direction being very narrow. Occasionally a cell closing in the pore longitudinally will be somewhat elongated vertically. This is comparable with the very elongated longitudinal cells bounding the pore in *Taxodium distichum*, in the vertical direction. The stomata in a band are very close, and frequently no epidermal cell separates two poral rings of adjacent lateral rows. At the most they are separated by one or two cells.

Epidermal Cells are elongated parallel to the long axis of the leaf. The cross walls show varying degrees of obliquity and are sometimes curved. This obtains also in *Taxodium europæum*, but to a much less extent in *Taxodium distichum*, though it also occurs there.

COMPARISON BETWEEN THE LEAVES OF

<i>Taxodium europæum</i> .	<i>T. distichum</i> .	<i>Glyptostrobus heterophyllus</i> .
<i>External Characters</i> .		
Leaves imbricated, closely adpressed; decurrent, and alternate.	Leaves deciduous, distichous, green, not scale-like.	Leaves persistent, spiral, closely packed, decurrent.
Leaves recurved, small, acute or obtuse. Size and form somewhat variable, scale-like or not.	Uninerved, light green needles.	Leaves recurved.
<i>Average length of leaf</i> .		
2·2 mm.	8·8 mm.	8 mm.
<i>Average width of leaf</i> .		
·57 mm.	1·0 mm.	·8 mm.

<i>Taxodium europæum.</i>	<i>T. distichum.</i>	<i>Glyptostrobus heterophyllus.</i>
<i>Cuticular Structure:—</i>		
<i>Stomata.</i>		
Arranged in bands occurring on both surfaces. Each band consists of 4-5 rows of stomata. Stomata sunk beneath epidermal pores.	Two bands on the lower surface. Not organised into definite bands on the upper surface. Stomata sunk beneath epidermal pores.	Banded arrangement of stomata, which occur on both surfaces. Stomata sunk beneath epidermal pores.
<i>Poral Axes.</i>		
Orientation mainly vertical, but oblique and transverse orientation also occurs.	Orientation of stomatal axes mainly transverse, but oblique and vertical orientation quite common.	Orientation very variable, but many orientated vertically.
Length .0104 mm. Width .0061 mm.	.02 mm. .008 mm.	.043 mm. .013 mm.
<i>Stomatal Pores.</i>		
Pores commonly surrounded by 4 epidermal cells. Five epidermal cells less commonly surround the pore.	Pores commonly surrounded by 4 epidermal cells, but 5 may occur forming then a rosette. Two out of the 4 are most clearly differentiated.	Pores commonly surrounded by 4, 5, or 6 deeply staining epidermal cells. Five cells forming a rosette round the pore occur most commonly.
When 4 epidermal cells surround the pore, two are orientated transversely and two longitudinally.	When 4 epidermal cells surround the pore, two are orientated transversely and two longitudinally.	When 4 cells surround the pore, they are not grouped as in <i>T. distichum</i> , but two may occur on each side.
<i>Epidermal Cells of the Poral Ring.</i>		
		The epidermal cells of the poral ring vary much in size, and one may be much larger than the others and be produced at one end like a horn. Av. length of the longest cell of the ring036 mm. Av. width of the longest cell of the ring014 mm. Av. length of the smallest cell of the ring028 mm. Av. width of the smallest cell of the ring014 mm.
<i>Epidermal Cells.</i>		
Elongated parallel to long axis of leaf.	Orientation mainly vertical, some amount of obliquity seen.	Orientation mainly vertical.
Length .039 mm. Width .017 mm.	Length .08 mm. Width .026 mm.	Length .1 mm. Width .023 mm.

It is evident from a comparison of the two leaf-cuticles that *Taxodium europæum* is a true *Taxodium*, and not a polymorphic form of *Sequoia*. Its likeness to *Taxodium distichum* appears to be very close, but the differences

are quite sufficient to warrant its specific separation, though they are differences of degree, rather than kind, and in so far as epidermal structures are evidence, it appears to be a synthetic form combining many of the characteristics of *Taxodium distichum* and of *Glyptostrobus heterophyllus*, which seem, as far as cuticular structure goes, to have diverged from it in two different directions, *Glyptostrobus* adopting the rosette type of pore, and *Taxodium distichum* the quadrangular type, both of which occur in the fossil form.

SUMMARY.

In the first part of this paper three distinct species of dicotyledonous leaves are described from their cuticular structures for the first time, namely: *Dicotylophyllum Stopesii*, *D. spiculatum*, and *D. sinuatum*. The name "*Dicotylophyllum*" is proposed for dicotyledonous leaves of uncertain affinity. The line of attack followed, in the attempt to obtain some insight into the flora, is the investigation of the cuticular structure, since that gives the next best results for comparison when the state of preservation of the material precludes the examination of the internal tissues.

In the consideration of the cuticles of the leaves selected, the features chosen for comparison are those visible in surface views, for in the case of the present material it was found to be impossible to obtain good sections through the cuticles.

The second half of the paper deals with the cuticles of certain gymnospermous fossil leaves. They are compared with known recent and fossil forms. *Araucarites Höpperti* appears to be a true *Araucaria* and far more closely resembles *A. excelsa* than *A. Cunninghamii*.

Taxodium europæum appears to resemble both *Taxodium distichum* and *Glyptostrobus* in its cuticular structure, which is quite different from that of the recent and fossil *Sequoias*. Hence it is very unlikely to be a polymorphic form of *Sequoia*, and shows most likeness to the genus *Taxodium*.

Sequoia Tournalii is seen to be less like *Sequoia sempervirens* in its cuticular structure than its external form would lead us to suppose, and its present position must be regarded as still open to question, though its cuticular structure shows certain points of likeness to that of *Sequoia sempervirens*.

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(Thesis approved for the Degree of Master of Science, London University.)

EXPLANATION OF THE PLATES.

Except where otherwise stated, the figured specimens are the property of the writer.

PLATE 20.

Fig. 1. *Dicotylophyllum Stopesii*, sp. n., natural size.

Fig. 2. Cuticle of under epidermis $\times 90$. Vein shown bearing hair bases. Hair bases are also seen among the stomata. Hair bases show cells with strongly thickened radial walls.

Fig. 3. Cuticle of under epidermis $\times 540$. Large guard cells with very thick cuticular rims, and open pores. Stomata surrounded by 4 or 5 definitely grouped accessory epidermal cells.

Fig. 4. Cuticle of upper epidermis $\times 90$. Parenchyma with hair bases and very few stomata.

Dicotylophyllum spiculatum, sp. n.

Fig. 5. Under epidermis $\times 90$. Stomata with open pores. Some apertures on the left of the field appear cruciform. V. 15863 a.

Fig. 6. Cuticle of under epidermis $\times 250$. Spicular ridges in accessory cells and epidermal cells. Asymmetry and irregularity in size of epidermal cells, and relatively greater width than length of accessory cells.

Fig. 7a. Cuticle of under epidermis $\times 540$. Thick-walled epidermal cells and branched spicules in four groups in accessory cells.

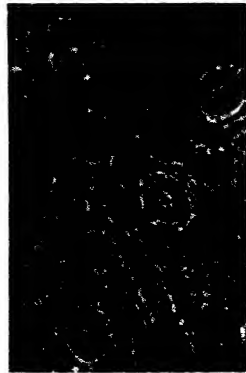
Fig. 7b. Cuticle of under epidermis $\times 540$. One stoma with accessory cells showing two groups of bifurcating spicules.

Fig. 8. Cuticle of under epidermis $\times 20$. Showing venation and angular silhouettes formed by stomatal cells which appear black, while the parenchyma appears light grey.

Fig. 9. Cuticle of upper epidermis $\times 90$. Thick-walled parenchyma without stomata.



10



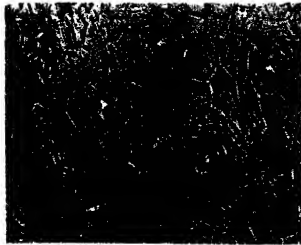
3



7b



12b



6



1



9



5



11



19



4

F.W.E. Phot.

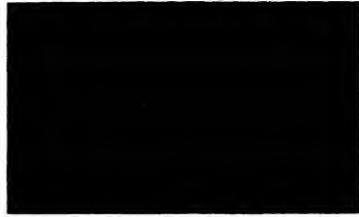
CUTICLES OF



12a



7a



18



15

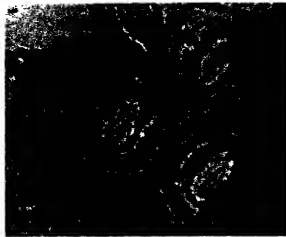


8



16

FOSSIL LEAVES



14



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2

17

F.W.E. Phot.



22



25



23



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20



31



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27



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35



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36

FOSSIL LEAVES

CUTICLES OF

Dicotylophyllum sinuatum, sp. n.

Fig. 10. Complete leaf, V.14917, British Museum (Nat. Hist.) (Geol. Dept.

Fig. 11. Under epidermis $\times 200$. Stomata grouped into areas by veins. Sinuate epidermal parenchyma. Thick-walled raised papillate hair bases on veins and scattered among epidermal cells. V. 15862 a.

Fig. 12 a. Under epidermis $\times 540$. Showing difference in size of pairs of guard cells and of pores. Thickened junction of guard cells is clear. A narrow granular subsidiary cell forms a border round each guard cell. V. 15862 a.

Fig. 12 b. Under epidermis $\times 540$. Showing collar-like hair base.

Araucarites Göpperti.

Fig. 13. Cuticle $\times 135$. Part of a stomatal band, in which stomatal axes exhibit great variability in orientation. Pores are surrounded by 4 or 5 accessory epidermal cells. V. 488 a.

Fig. 14. Cuticle $\times 380$. Guard cells within the poral ring of accessory cells. Thick-walled epidermal cells, horizontally elongated, occur between two adjacent stomata in one linear series. V. 488 a.

Araucaria Cunninghamii.

Fig. 15. Cuticle $\times 135$. Band of closely-packed stomata whose axes vary in direction, and thick-walled sinuate oblong epidermal cells.

Fig. 16. Cuticle $\times 380$. Two stomata with accessory cells. Thick-walled pitted epidermal parenchyma surrounds the poral rings.

Araucaria excelsa.

Fig. 17. Cuticle $\times 135$. Part of stomatal band showing asymmetric poral axes, and rather irregular stomatal lines. Narrow, vertically elongated, straight-edged epidermal cells between the stomatal series.

Fig. 18. Cuticle $\times 380$. Two epidermal pits surrounded by 4 (or 5 in one case) accessory cells, and with guard cells below the surface. Stomatal pore between the guard cells is seen as a narrow slit.

Araucaria Bidwillii.

Fig. 19. Cuticle of under epidermis $\times 380$. Stomatal pit surrounded by 5 accessory cells, which disturb the symmetry of the vertical rows of epidermal cells.

PLATE 21.

Araucaria Bidwillii.

Fig. 20. Cuticle of under epidermis $\times 135$. Vertically orientated stomata in linear rows. Vertically elongated epidermal cells.

Araucaria imbricata.

Fig. 21. Cuticle $\times 135$. Thick-walled epidermal cells. Linear series of stomatal pits, whose axes vary in orientation.

Fig. 22. Cuticle $\times 380$. Four stomatal pores, one pore shows slightly open guard cells.

Sequoia gigantea.

- Fig. 23. Cuticle $\times 200$. Stomatal pores and epidermal cells of which the majority appear vertically orientated in this part of the leaf.
- Fig. 24. Cuticle $\times 540$. Part of fig. 23 enlarged, showing pores with 5 and 6 accessory cells.
- Fig. 25. Cuticle $\times 380$. One stoma with accessory cells.

Sequoia sempervirens.

- Fig. 26. Cuticle $\times 135$. Under surface. Part of a stomatal band. Note waved character of the epidermal and stomatal rows. Great length and narrowness of the midrib cells contrasts with epidermal cells between adjacent stomata.
- Fig. 27. Cuticle $\times 380$. Stomatal pits surrounded by 4 or 5 accessory cells, those vertically orientated are generally longer than those closing in the pore horizontally and some show horn-like projections.

Sequoia Tournalii. V. 15103 b.

- Fig. 28. Cuticle $\times 135$. Vertically orientated rows of stomata. Wide midrib.
- Fig. 29. Cuticle $\times 200$. Showing stomatal pits more clearly.
- Fig. 30. Cuticle $\times 380$. Showing slightly sinuate character of some of the cell-walls, and the presence of pits in the walls. Note the lack of sharp distinction between the accessory cells of the poral ring and the remaining epidermal cells.

Sequoia Couttsiae.

- Fig. 31. Cuticle $\times 135$. Part of a stomatal band with epidermal cells whose orientation, when situated between the stomatal rows, is mainly vertical, while some epidermal cells between adjacent stomatal pits show horizontal orientation.
- Fig. 32. Cuticle $\times 380$. Five epidermal pits are shown whose orientation is mainly vertical. Each pit is surrounded by 4 or 5 narrow elongated accessory cells.

Taxodium europæum. V. 15072 a.

- Fig. 33. Cuticle $\times 135$. Part of a stomatal band. Pores bounded by 4 or sometimes 5 accessory cells. Orientation of epidermal cells and poral axes is mainly vertical.
- Fig. 34 (see Pl. 20). Cuticle $\times 380$. One epidermal pit shown surrounded by rosette-like ring of 5 accessory cells.

Taxodium distichum.

- Fig. 35. Cuticle $\times 135$. Showing epidermal pits surrounded by 4 or 5 accessory cells. Poral axes show oblique and vertical orientation. The five cells may form a rosette.
- Fig. 36. Cuticle $\times 380$. Four epidermal pits with varying axial orientation, and variation in the grouping of the accessory cells of the poral ring.

Glyptostrobus heterophyllus.

- Fig. 37. Cuticle $\times 135$. Part of two stomatal bands, one from the upper and one from the lower surface of the leaf. Poral rings consist of 4, 5, or 6 accessory epidermal cells. Orientation of the poral axes variable. Epidermal cells are vertically orientated.
- Fig. 38. Cuticle $\times 540$. Three poral rings with variable orientation bounded by 4, 5, and 6 accessory cells. Note the horn-like prologation of two of the accessory cells. The junction of the guard cells shows as a slit, or partly open pore.

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The Genus *Polysiphonia*, Grev., a critical Revision of the British species, based upon Anatomy. By LILY BATTEN, M.Sc., Ph.D. (Communicated by Prof. Dame HELEN GWYNNE VAUGHAN, D.B.E., D.Sc., F.L.S.)

(PLATES 22-25.)

[Read 14th December, 1922.]

THE object of the following paper is to work through critically the British species of *Polysiphonia*, but at the same time to investigate thoroughly their organs of attachment. An attempt having been made to collect material from various localities, the neighbourhood of Swanage was finally decided upon as the special area for purposes of this paper, a series of visits being subsequently made at different times of the year. The nature of the rock and tilt of the strata was found to influence the distribution of marine algæ, even if one only considers the mechanical action of the water. The area chosen is very varied geologically, so that species can be found which need sheltered bays for their habitation, as well as those which are able to persist on rocky headlands exposed to the full force of the tide. Studland is a sheltered bay, eroded in sandy Tertiary beds. It is not only valuable for its own flora, but for the numbers of specimens which are washed into the bay after rough weather. West of Ballard Down the Wealden is exposed, the beds consisting of sand and clays, while between Durlston Head and St. Alban's Head the Portlandian forms the coast-line, 19 feet of Portland stone forming the base of the cliffs in Durlston Bay. The mud flats of Poole Harbour form another type of hunting-ground, where local conditions cause marked variability in the form of certain species. In the marine lake of Poole Park a floating form of *P. variegata* has been found and given to me for description by Mr. A. D. Cotton. Between the Haven, at the entrance of Poole Harbour, and Sandbanks, a number of groins run out into the sea, and these are particularly rich in some of the smaller Polysiphonias.

Material which can only be obtained by dredging has been sought after at Plymouth from the 'Oithona,' belonging to the Marine Biological Station, and useful shore-collecting for individual species has been done near Wembury and on the island off Looe, as well as at Ilfracombe, Torquay, and near Berry Head. A few rare species which it was not possible to obtain by collecting have been examined at the Royal Botanic Gardens, Kew, the Natural History Museum, South Kensington, and in the herbarium of Mrs. Griffiths at Barnstaple.

Former systematic descriptions of the group have been worked through critically, attention having been paid to the general detailed anatomy of the

thallus, which in many of the essential points is curiously similar throughout the genus. The study of the attachment organ has been of considerable interest, largely on account of the gradual increase in complexity which is visible in the group. The form of the attachment organ has been correlated with the general anatomy of the species, and the parasitism of *P. fastigiata* has been proved.

The elimination of false synonyms has been possible after consulting the records and collections at Kew and the Natural History Museum. An attempt has also been made to bring together those plants which are forms of some previously recorded British species, but through environmental modification have been given a new specific name, or have been re-named by British workers without due consultation with the records of foreign species. A key to the species, based on purely vegetative characters, has also been compiled, and *P. spiralis* is described for the first time. In order that the paper may be more complete for reference, a summary of the literature on the development of the reproductive organs of the genus has been inserted.

The paper deals exclusively with the genus *Polysiphonia*, of which 24 species are recorded, types which are now grouped with the *Pterosiphonias* having been reserved. The two groups are distinguishable by their respective methods of branching. In the *Pterosiphonias* the branching is markedly pinnate throughout the plant, both branches and ramuli being set at acute angles.

My thanks are due to Professor O. V. Darbishire for his advice and help, and for having placed his valuable library at my disposal. I am also indebted to Mr. A. D. Cotton for material from Weymouth and Poole, to Mr. W. Searle for specimens from Looe and Plymouth, and to Mr. W. P. Hiern for specimens of *P. variegata* and *P. subulifera* from the herbarium of the Rev. W. S. Hore, and for his kindness in facilitating my access to the herbarium of Mrs. Griffiths at Barnstaple. I must also express my thanks to Miss Blackburn for material from Cullercoats, to Dr. A. H. Church, and to Mr. E. M. Holmes for valuable information. Any artistic merit which the figures may possess is largely due to the experienced advice and criticism of my friend, Mr. C. Hanney, of the Bristol School of Art.

I should also like to take this opportunity of expressing my thanks to the Committee for Industrial and Scientific Research, and to the Colston Research Committee for financial assistance.

HISTORICAL.

The genus *Polysiphonia* was originally described by Agardh in 1817 under the name of *Hutchinsia*, but that name is inadmissible owing to a group of the Cruciferae having been previously given that generic name by Robert Brown. In 1822 Bonnemaison substituted the term *Grammita* for that of

Hutchinsia. This, however, was objected to by Greville (Fl. Edinensis, 1824, p. 308) owing to the possibilities of confusion with *Grammitis* which had already been used for a group of Fungi, and by Swartz in 1801 for a genus of Ferns, which was a synonym for *Polypodium*. Greville therefore devised the term *Polysiphonia*, which has persisted in spite of the indignation of Desmazières (21), who was reluctant to abandon the term which had the privilege of seniority, for one "qui paraît devoir son existence au caprice."

MORPHOLOGY.

The *Polysiphonia* plant consists of a branched thallus, bearing numerous ramuli. In perennial forms like *P. elongata* the ramuli are shed annually before the winter, the plant being re-clothed in the spring. At the tips of the branches and of the ramuli, clusters of fine filamentous hairs are borne in many species, and on these the antheridia are produced. Tetraspores are borne in the ramuli, and cystocarps may be developed either on the ramuli or on the branches of the thallus. The attachment of the plant is effected by the development of numerous rhizoids.

ANATOMY.

The species are divisible into two main groups :—

- (a) Ecorticate,
- (b) Corticate.

The anatomy of the ecorticate forms consists solely of siphons, that is of cells which extend the whole length of the articulation (Pl. 22. fig. 5). In the corticate forms, however, in addition to the siphons, there are cells present at the periphery of the thallus which are much shorter than the siphons and smaller in diameter. These form a mosaic which may extend over the whole plant as in *P. fruticulosa*, or may only occur on the lower parts as in *P. violaceu* (Pls. 25, 24. figs. 78, 59).

The thallus consists throughout the group of one central siphon and a band of primary pericentral siphons numbering from 4 to 20 or even more. These may be surrounded by alternating bands of smaller siphons, and bounded externally by one or more rows of cells, in the corticate forms. The pericentral siphons are usually parallel to the main axis. In *P. atrorubescens*, *P. nigrescens* var. *ε. affinis*, and occasionally in *P. fibrata*, however, a slight spiral formation is visible, and the same phenomenon is well defined in what is believed to be a new species, and has been here described as *P. spiralis*.

P. urceolata will serve to typify the ecorticate species. The thallus consists here of one central siphon, and four pericentral in each articulation. The central siphon is much smaller than the pericentral ones, and there is protoplasmic continuity throughout the plant. The upper and lower ends of the siphons are connected by almost colourless strands of protoplasm, which

contain very few granules, and which pass through a lenticular patch in the adjacent end-walls of contiguous cells. In the central siphon this connecting filament is rather larger than in the pericentral, and is deeper in colour. At the point through which the protoplasm passes there is a lenticular thickening round the margin of the aperture, while the actual diaphragm is like a perforated plate (Pl. 22. fig. 1). There is also a lateral connection of the central with the pericentral siphons on the tangential walls. The form of the connection is uniform throughout, but the lateral connections are not necessarily at a uniform level throughout the articulation, during the whole life of the plant.

Each siphon contains a mass of pink protoplasm, embedded in which are a number of red chromoplasts. The plastids are not so numerous in the central siphon, and in the pericentral ones they are usually arranged near the periphery of the thallus. The nucleus does not stain very readily, but after prolonged treatment with iodine may be observed in the younger parts of the thallus, where it is very large compared with the diameter of the cell (Pl. 22. fig. 3).

The apical cell is a rounded and flattened cone, filled with granular protoplasm and containing a large nucleus. When growth proceeds, a thin disc is separated by a wall from the base of the cone, but the wall is perforated in five places, through which strands of protoplasm pass, one central and four pericentral strands. At a later stage there is a longitudinal fission of the disc into a central mass and four pericentral portions. The four pericentral parts then become separated longitudinally by walls, but retain a protoplasmic connection longitudinally and laterally with the contiguous siphons and the central siphon respectively. As Massee has pointed out (42. p. 198 *et seq.*), the increase in size of a *Polysiphonia* is the result of two methods of cell formation. The axial row of siphons by which the thallus increases in length is the result of the division or segmentation of the apical cell, while the increase in thickness is due to "gemmation" from the axial cells.

There is a slight variation of form in the thallus of *P. fastigiata*. In the young state the protoplasm of the central siphon fills the whole cell-cavity. Later, however, the wall becomes thickened, particularly in the upper and lower parts of the siphon. As a result the cell contents are shut down into a flattened mass, which is connected with the central siphons above and below by a narrow strand of protoplasm passing through the thickened walls (Pl. 22. fig. 4). In this case the pericentral siphons are connected with the central at a uniform level in each individual articulation, the protoplasmic strands penetrating the wall and uniting with the protoplasm of the central siphon. There is a well-defined thickened rim visible at the point through which the protoplasmic strand passes from one cell into the next. There has been a considerable amount of controversy as to whether these openings are maintained in the older state of the plant. Schmitz (50. p. 215) considers that

protoplasmic continuity is maintained throughout the life of the cells. Masee (42. p. 198) thinks that the opening becomes closed by the growth of a cellulose plate, to the margin of which the primordial utricle is attached. He considers, however, that fine protoplasmic threads pass through minute holes in the plate, and so maintain the continuity of the protoplasm. Harvey Gibson (27. p. 129) has shown, however, that in *P. fastigiata*, at any rate, the canal is closed in the older parts of the plant. Fine granular striæ are visible, but maceration shows these to be a fringe of fine threads arising along the margin of the plug and quite independent of the protoplasmic contents of the canal.

The structure of the corticate species is similar to that of the ecorticate, but in addition to the formation of the primary pericentral siphons in the manner described for *P. urceolata*, there may be an additional formation of secondary and tertiary siphons by "gemination" from the primary and secondary respectively. When small cells are developed round the periphery these are produced from the outermost layer of the siphons in a similar manner. This is particularly well seen in *P. elongata*, where protoplasmic continuity is clearly visible in a median longitudinal section of the thallus. In some of the large corticate forms of which *P. elongata* is typical the system of protoplasmic continuity is more complex than in the ecorticate species. In the very early stage there is one connection at each end of the central siphon, but as the plant increases in size, four strands are developed round the central one in each central siphon, while additional strands also occur in the pericentral siphons. If there is more than one row of corticating cells at the periphery, the outer layers are formed by gemination from the inner, and protoplasmic connections are maintained.

The mode of branching is variable throughout the group. It may be monopodial, axillary, or pseudo-dichotomous. Rosenvinge (35. p. 222) investigated the development of *P. violacea*. He found that in this axillary type the two daughter-cells of the apical cell are unequal in size, giving the impression that the smaller cell is cut off from the larger. In *P. fastigiata*, however, very marked pseudo-dichotomy is visible. The apical cell is divided by two oblique walls, and the branches grow out on either side at right angles to the inclined septa.

ATTACHMENT ORGANS.

The Polysiphonias are usually attached, the only exception being occasional floating forms of particular species. A floating form of *P. variegata* was found in the marine lake of Poole Park, and is described on page 308.

The substratum varies with the species, and may be rocks, stones, shells, wood, or other algæ. When growing on other algæ the Polysiphonias are epiphytic, with the exception of *P. fastigiata*, which derives food from its host *Ascophyllum nodosum*. The usual type of attachment organ is formed of a

number of rhizoids, which may or may not develop discs at their distal ends, depending on the nature of the substratum. The formation of these rhizoids presents a feature of considerable interest, as a gradual increase of complexity is traceable, which can be correlated with the anatomy of the species.

The rhizoids are thick-walled, and are formed principally by the lateral proliferation of primary pericentral siphons in ecorticate forms such as *P. macrocarpa*. In corticate forms, however, where the thallus is bounded by small cells, the rhizoids are formed from these latter, and not from the siphons themselves. Fig. 5 (Pl. 22) shows the development of a single rhizoid from a pericentral siphon in *P. macrocarpa*. The formation of rhizoids from the corticating cells of *P. nigrescens* is shown in fig. 6 (Pl. 22). When the rhizoids ramify among the small filamentous algæ and debris on the surface of a rock, they do not develop discs at their extremities (Pl. 25. fig. 64). If, however, the tip of the rhizoid comes into contact with some firm object such as a fragment of rock or shell, or some larger alga, a flattened expansion begins to form. This eventually becomes lobed, but no septation takes place (Pl. 22. fig. 2). The formation of a disc is a direct response to the stimulus of contact. If the rhizoid attaches itself to a sand grain, the disc bends over and partially encloses the grain. Derick (20. p. 251) states that the rhizoids of *P. violacea* are separated from the corticating cells by a wall, but I have never observed a wall at the base of a rhizoid in any species of *Polysiphonia* that I have examined. The rhizoids are unicellular, and are usually unbranched, but in *P. urceolata* an occasional tendency to branch may be observed although no septation takes place.

Where *Polysiphonia* grows on another alga epiphytically, as, for example, *P. violacea* on *Chorda filum*, rhizoids are formed which adhere to the surface of the host by means of their expanded discs. Penetration does not take place, but the host is frequently a little distorted, and has fewer chromatophores in the part of the thallus below the discs.

The question naturally arises as to the exact means by which the disc is attached to the substratum. It must adhere either like a sucker, or by the purely mechanical means of fitting in among the crevices of the substratum, or by the secretion of a cement. Careful observation and sections have failed to reveal any lifting of the centre of the discs either individually or in the aggregate, and the presence of large forms like *P. elongata* on a perfectly smooth water-worn pebble near a jetty, seems to indicate, that purely mechanical adherence by fitting in with the crevices of the substratum is an inadequate explanation. Where the substratum is irregular, this latter method no doubt aids in the attachment, but it is not sufficient when acting alone on certain substrata. It appears, therefore, that the thickened discs consist partly of a cementing substance which helps to fix the alga. It was suggested that there might be some chemical combination of the secretion with the substratum, but I have been unable to find any trace of chemical

change in cases where examination proved possible. It seems most probable that the alga adheres largely by the action of its own gelatinous wall membrane, the formation of the disc giving increased surface for attachment.

A modification of the disc occurs in *P. fastigiata*. The rhizoids actually penetrate the tissues of the host, and at the tip the wall is thin and the cell is filled with granular contents. If a section of the *Ascophyllum* thallus be taken, it is noticeable that certain of the host cells near the tip of the rhizoid are darker in colour than their neighbours, and that similar dark cells are present at places where the rhizoid has passed at an earlier stage. A number of sections were taken, and the rhizoid-tip was found closely applied to certain darkened *Ascophyllum* cells. This suggested that the rhizoid attacked these cells, the swollen tip acting as an haustorium (Pl. 22, figs. 7, 8). Rattray (48) believed that a partial parasitism must occur in the association, and Tobler-Wolff (55) observed the dark cells, but no definite statement of parasitic habit was made in either case.

With a view to ascertaining whether the contents of the *Ascophyllum* cell had been changed by contact with the *Polysiphonia*, a chemical test was applied. *Ascophyllum nodosum* does not contain starch in the form in which it is usually found, but the food-store stains red when treated with a solution of vanillin in concentrated HCl. Sections were therefore placed for a moment in the solution, then washed and examined in water, and it was found that the contents of the ordinary *Ascophyllum* cells became bright red, whereas the dark cells gave no reaction. It is evident, therefore, that the *Polysiphonia* obtains food from the cells of the host which it attacks (Pl. 22, fig. 8).

Where there is an extensive growth of the parasite, the *Ascophyllum* frequently has a somewhat stunted and more rigid thallus in the immediate neighbourhood of the *Polysiphonia*. This, however, is probably due to some extent to the increased strain to which it is subjected, with an increased surface for the action of the waves, and is not solely due to the semi-parasitic habit of the *Polysiphonia*. As Rattray (*loc. cit.*) has pointed out, it is not absolutely necessary for the life of *P. fastigiata* that it should be fixed to any host, as it occurs, though comparatively rarely, growing on a rocky substratum. When this happens, however, its vegetative growth is less perfect, although it may be exposed to similar conditions with regard to depth and general environment. The fact only bears out the view that a direct advantage is gained by an epiphytic habit.

In order to illustrate the degree of complexity which is visible in the attachment organs of the genus, four types may be selected.

1. *P. urceolata*.

The young plant is usually attached to the substratum by two rhizoids which are developed by longitudinal proliferation of the base of the primary

siphons ; the actual number is, however, subject to slight variation. These rhizoids are terminal in origin, and not lateral like the subsequent ones. As growth proceeds and the thallus branches, any pericentral siphon of a procumbent branch may develop a rhizoid, and thus afford additional strength for the attachment of a colony. Ultimately then, the colony is attached by a large number of rhizoids which arise from the main axis and low branches, but there is no aggregation into any special form.

In this type of attachment the tips of the rhizoids may ramify among the algæ and debris, and not become expanded as in the figure of *P. fetidissima* (Pl. 25. fig. 64), or they may develop expanded discs as in *P. urceolata* itself, or become swollen as haustorial organs, as in *P. fastigiata*.

2. *P. nigrescens*.

The main principle of the attachment is similar to that of *P. urceolata*, but at the extreme base of the thallus a row of corticating cells frequently occurs. This appears to be correlated with the closer development of rhizoids, and the fact that an aggregation is possible whereby the discs of the colony adhere mechanically to each other, making an uninterrupted surface at the base of the attachment. This mechanical coherence of the discs is not so marked in the ecorticate species of *Polysiphonia*, and it appears that the phenomenon is made possible by the presence of the corticating cells and consequent closer development of the rhizoids, and is also facilitated by the presence of a greater number of pericentral siphons than is present in the group typified by *P. urceolata*. It appears to be the first step towards the aggregation of the individual discs into a single large attachment organ, such as is seen in *P. elongata*, but there is no sign of the coalescence of the upper parts of the rhizoids.

3. *P. fruticulosa*.

P. fruticulosa is corticate throughout, and rhizoids are formed in large numbers from the corticating cells. There is, however, a special adaptation which is of interest. The young plant is attached at the base by a number of terminal rhizoids. When branching takes place, certain of the lower branches are procumbent for a short distance, and themselves branch alternately as they creep along the substratum. Of these secondary branches, the upper ones continue growth in an upward direction, while those on the under side of the thallus become stunted and short. The corticating cells of these stunted branches send out large numbers of rhizoids, and the whole branch appears to be devoted to the function of attachment (Pl. 25. fig. 78). The tip of the branch frequently bends round the thallus of any small alga which it may encounter, and thus affords additional strength. A few rhizoids may develop from the procumbent parts of the original branches, but the principal means of attachment is the modified branchlet. There is no mechanical

cohesion of the upper parts of the rhizoids, but the expanded bases may fit in together, though I have never found a definite plate such as one sees in *P. nigrescens*.

4. *P. elongata*.

P. elongata is typical of the most complex form of attachment which is exhibited in the genus. A median longitudinal section shows that the siphons themselves, as well as the corticating cells, take part in the formation of the large disc by means of which the plant is attached (Pl. 24. fig. 47). The central and pericentral siphons, together with a large number of corticating cells, are elongated longitudinally into rhizoids, and as elongation takes place, the cells and siphons at the base spread out, so that a bigger surface is available for attachment. The outer rhizoids develop discs comparable to those of *P. urceolata*, but the discs of the inner rhizoids are smaller on account of crowding. The upper parts of the latter mechanically coalesce to form a pseudo-tissue, and it is only on the outside at the extreme base of the attachment that the separate walls of individual rhizoids may be discerned. With this form of attachment it is only the base of the main axis which is involved, so that none of the branches are procumbent, and consequently plants with an individual axis are characteristic, instead of a colony as in *P. nigrescens*.

Taking these four species as typical of the groups which they represent, it is apparent, therefore, that the more complex type of attachment organ can be correlated with the development of cortication in the genus. In the simple ecorticate forms the attachment organ consists of rhizoids which are developed by the proliferation of the siphons themselves. As cortication begins to be visible, the smaller outer cells form the attachment, and there are signs of an aggregation into disc-like form. When the whole plant is corticate, the attachment is either formed by means of a modified branch as in *P. fruticulosa*, or the siphons and corticating cells take part in the formation of a disc as in *P. elongata*. Intermediate forms occur, as for example *P. Brodiaei*, where the original disc is comparable to *P. elongata*, but the procumbent branches afford additional mechanical strength by sending out rhizoids at their bases.

REPRODUCTION.

Tetraspores.

Tetraspores are borne in the ramuli, and may either occupy the tip of the ramulus, as is usual in *P. urceolata*, or may be intercalary in development as in *P. Brodiaei*. As Masee (42. p. 198 *et seq.*) has pointed out, the tetrasporangium originates in the same way as the pericentral siphons, and in *P. fastigiata* occupies a space equal to that occupied by two siphons. Two daughter-cells are developed on the outside by gemmation from the tetrasporangium (Pl. 22. fig. 9), which is in communication with the axial siphon

by a protoplasmic strand. The tetrasporangium divides into two transversely, the basal cell remaining inconspicuous, while the upper one grows rapidly. The wall becomes definite and the contents assume a dark colour. The nucleus of the tetraspore mother-cell has been shown by Yamanouchi (62. p. 401 *et seq.*) to contain 40 chromosomes, and as a result of reduction division the nuclei of the tetraspores contain only 20. After the division of the nucleus, the contents of the mother-cell divide into four parts, which arrange themselves in a definite way. One remains at the base of the cell near the point of communication with the basal cell, two occur over this one, and the fourth at the top of the large oval cell. As the tetraspores increase in size, the neighbouring siphons become pushed outwards, resulting in a distorted ramulus.

Antheridia.

The antheridia are developed at the tips of the branches, where they either replace the whole of one of the jointed filamentous hairs, or else one arm of the first branch of a dichotomous hair. In material of *P. nigrescens* from Plymouth Sound each antheridium replaced an entire hair, and the filamentous axis was continued for a considerable distance beyond the tip of the antheridium. The antheridia are elongated, somewhat cylindrical, and often slightly curved. The structure of the antheridium has been described by Yamanouchi (62. p. 401 *et seq.*). A filamentous axis extends down the centre, and on this the flattened stalk cells are borne. The sperm mother-cells which give rise to the antherozoids are formed on the stalk cells, and large numbers of oval sperms are developed, each containing a large vacuole.

Cystocarps.

The development of the cystocarp has been worked out in detail by Phillips (46 & 47. pp. 289-301), Schmitz (50), Yamanouchi (62. p. 401 *et seq.*), and others. Oltmanns (44. p. 99 *et seq.*) showed that the real sexual act is the union of the male and female gamete nuclei in the carpogonium, and that the auxiliary cells are probably only concerned with the nourishment of the cystocarp. Previous to this work, the act of fertilization and the secondary fusions concerned with the auxiliary cells were all included in the sexual process.

According to recent work by Yamanouchi (*loc. cit.*) and Phillips (*loc. cit.*), the procarp in *P. violacea* consists in the beginning of a short branch of three or four cells. The most important of these is the cell of the axial siphon lying next to the apical cell. This divides to form five pericentral cells, which completely surround it. One of these is the "pericentral cell," which will give rise to the carpogonial branch. The nucleus of the pericentral cell divides nearly parallel to the axis of the procarp, cutting off a cell which develops the carpogonial branch. The pericentral cell later gives rise to a group of auxiliary cells. The carpogonial branch consists of four cells, the terminal of which becomes the carpogonium and develops a trichogyne.

The nucleus of the carpogonium divides to form two nuclei, one of which becomes the female gamete nucleus; the other enters the trichogyne, which becomes elongated and constricted where it joins the carpogonium.

When a spermium becomes attached to the tip of the trichogyne, the walls between dissolve and the contents of the sperm enter. The sperm nucleus, which contains 20 chromosomes, passes into the carpogonium; the male and the female nuclei lie in close proximity, while the trichogyne nucleus disintegrates and the trichogyne shrivels. The nuclei in the carpogonium fuse, and a set of auxiliary cells are developed by the pericentral cell round the fertilized carpogonium. With the fusion of the two nuclei the number of chromosomes is brought up to 40, and the sporophyte generation has begun. The carpogonium then fuses with the auxiliary cell, which lies between it and the pericentral cell. A fusion with the pericentral cell itself follows immediately, and the fused sexual nucleus, which has divided into two, moves down to the pericentral cell. After this, the passage between the carpogonium and the auxiliary cell closes, and the carpogonium remains isolated, finally breaking down with the three sister-cells of the carpogonial branch. During the formation of the auxiliary cells from the pericentral cell, each nucleus in the first three cells of the carpogonial branch divides, the daughter-nuclei lying side by side in pairs. The protoplasmic connection which exists between the auxiliary and pericentral cells becomes larger, and the nuclei of the auxiliary cells move towards the pericentral cell. This general union results in the formation of a large cell, which was called by Phillips (46. p. 289) the "central cell." It contains many nuclei, two of which are sporophytic, the others gametophytic. The sporophytic nuclei divide and the central cell develops lobes, into each of which a sporophytic nucleus passes. The nuclei again divide, and a carpospore is cut off terminally, the lower part remaining as a stalk cell, attaching the carpospore to the central cell. After the formation of the carpospores, the central cell increases in size greatly, absorbing the stalk cells. The envelope of the cystocarp is developed from the peripheral siphons of the original procarpic branch, and is lined with delicate filaments, the paranemata, which arise from the cell of the axial siphon. The cystocarp is urn-shaped, with an ostiole at the top, through which the carpospores are discharged.

SUMMARY.

Species of British *Polysiphonia* may be classified according to their anatomical differentiation. The thallus consists of a central siphon, surrounded by four or more pericentral siphons. In the corticate forms, external cells are also present which do not extend for the complete length of an articulation. Protoplasmic continuity is present throughout the plant in the young stages, although later some of the connecting pits may become closed.

Growth takes place by two methods of cell formation—division from the apical cell and “gemmation” from the axial cells.

The form of the attachment organ varies with the species, and is influenced by the nature of the substratum. Four types may be distinguished :—

1. The ecorticate plant is originally attached by rhizoids, which are developed from siphons by longitudinal proliferation. Later, siphons of procumbent branches also develop rhizoids. Rhizoids may have discs at their distal ends when they encounter a hard substratum, or may ramify among filamentous algæ without expanding, or may be swollen to form haustoria in certain species.

2. Species having a number of siphons or a beginning of cortication at the base show elementary aggregation of the rhizoids to form a large disc, the expanded tips of the rhizoids themselves interlocking mechanically. Procumbent branches also develop rhizoids which give additional strength, and the cells as well as the siphons aid in the formation of the attachment organ.

3. *P. fruticulosa*, which is originally attached by a number of longitudinally developed rhizoids, and, later, certain procumbent branches which are stunted function specially in the formation of the attachment organ.

4. Species with an upright habit, which do not branch near the base, develop a large disc-like expansion at the base of the thallus. Such forms are always corticate. The siphons and corticating cells at the base all grow downwards longitudinally and form rhizoids. The rhizoids cohere mechanically with each other, so that a pseudo-tissue is formed.

Sexual and asexual organs of reproduction are present in the group. Tetraspores are either intercalary or are borne terminally. The tetrasporangium originates in the same way as the pericentral siphons, subsequently dividing into two, the upper of which develops four tetraspores.

Antheridia are borne at the tips of the branches and ramuli, each antheridium either replacing a filamentous hair or one arm of a dichotomous hair.

Cystocarps are borne on the branches and ramuli. They are urn-shaped, with an ostiole at the top, which is occasionally sinuous and through which the carpospores are discharged.

A classification and description of the individual species follows, together with a key for identification.

ENUMERATION AND CLASSIFICATION OF SPECIES OF *POLYSIPHONIA* ACCORDING TO THEIR ANATOMICAL DIFFERENTIATION.

I. Ecorticate Species.

A. Four primary pericentral siphons.

- | | |
|---------------------------|--------------------------|
| 1. <i>P. insidiosa</i> . | 4. <i>P. spiralis</i> . |
| 2. <i>P. macrocarpa</i> . | 5. <i>P. urceolata</i> . |
| 3. <i>P. rhunensis</i> . | |

B. More than four primary pericentral siphons.

- | | |
|------------------------------|---------------------------|
| 1. <i>P. atro-rubescens.</i> | 5. <i>P. opaca.</i> |
| 2. <i>P. fastigiata.</i> | 6. <i>P. Richardsoni.</i> |
| 3. <i>P. furcellata.</i> | 7. <i>P. simulans.</i> |
| 4. <i>P. obscura.</i> | 8. <i>P. subulifera.</i> |

II. Corticate Species.

A. Four primary pericentral siphons.

- | | |
|-------------------------|--------------------------|
| 1. <i>P. elongata.</i> | 4. <i>P. fibrillosa.</i> |
| 2. <i>P. elongella.</i> | 5. <i>P. spinulosa.</i> |
| 3. <i>P. fibrata.</i> | 6. <i>P. violacea.</i> |

B. More than four primary pericentral siphons.

- | | |
|---------------------------|--------------------------|
| 1. <i>P. Brodiaei.</i> | 4. <i>P. nigrescens.</i> |
| 2. <i>P. fatidissima.</i> | 5. <i>P. variegata.</i> |
| 3. <i>P. fruticulosa.</i> | |

KEY TO SPECIES.

- | | | |
|--|----|---------------------------|
| 1. Axis consisting of 4 primary pericentral siphons, with or without cortication | 20 | |
| More than 4 | 2 | |
| 2. Axis consisting of 5 primary pericentral siphons | 3 | |
| More than 5 | 4 | |
| 3. Articulations 3 or 4 times longer than broad in lower parts of axis; siphons spirally placed | | <i>P. Richardsoni.</i> |
| Articulations shorter than their breadth near the base; siphons irregular | | <i>P. variegata.</i> |
| 4. Axis consisting of 6 primary pericentral siphons, with or without cortication | 8 | |
| More than 6 | 5 | |
| 5. Axis consisting of 7 primary pericentral siphons, with or without cortication | 8 | |
| More than 7 | 6 | |
| 6. Axis consisting of 8-11 primary pericentral siphons, with or without cortication | 7 | |
| More than 11 | 11 | |
| 7. Zone of cells present in older parts, outside primary siphons. | 8 | |
| Not so | 9 | |
| 8. Ramuli slender and regularly distributed over the younger branches. Ramuli borne close together, giving plant a tufted appearance | | <i>P. variegata.</i> |
| | | <i>P. Brodiaei.</i> |
| 9. Pericentral siphons spirally curved | | <i>P. atro-rubescens.</i> |
| Not so | 10 | |
| 10. Colour bright brick-red | | <i>P. furcellata.</i> |
| Colour dark brownish-red | | <i>P. fatidissima.</i> |
| 11. Axis consisting of 12-14 primary pericentral siphons, with or without cortication | 12 | |
| More than 14 | 17 | |

12. Pericentral siphons spirally curved	<i>P. atro-rubescens.</i>
Not so	13
13. Maximum height of plant $\frac{1}{2}$ inch	<i>P. obscura.</i>
Not so	14
14. Plant corticate throughout	<i>P. fruticulosa.</i>
Not so	15
15. Colour bright brick-red when fresh	<i>P. subulifera.</i>
Not so	16
16. Central siphon small	<i>P. simulans.</i>
Central siphon occupying about half the radius of thallus in transverse section	<i>P. nigrescens.</i>
17. Filaments decumbent; plant not more than $\frac{1}{2}$ inch high	<i>P. obscura.</i>
Not so	18
18. Usually parasitic on <i>Ascophyllum nodosum</i> , and containing conspicuous central siphon	<i>P. fastigiata.</i>
Not so	19
19. Zone of corticating cells present outside the primary siphons at extreme base of main axis	<i>P. nigrescens.</i>
Axis consisting solely of about 20 pericentral siphons, and one central, ecorticate throughout	<i>P. opaca.</i>
20. Plant ecorticate	21
Plant corticate	28
21. Siphons spirally curved in principal branches	23
Not so	22
22. Plants gelatinous, occurring in tufts about 1 inch in height	<i>P. macrocarpa.</i>
Not so	24
23. Articulations one or $1\frac{1}{2}$ times as long as broad	<i>P. spiralis.</i>
Articulations 6-8 times as long as broad	<i>P. fibrata.</i>
24. Colour deep full red	<i>P. urceolata.</i>
Not so	25
25. Articulations 4-6 times as long as broad	26
Not so	27
26. Ramuli dichotomously branched	<i>P. fibrata.</i>
Ramuli alternate or unilateral	<i>P. insidiosa.</i>
27. Plant greyish in colour. Articulations 3 or 4 times as long as broad	<i>P. insidiosu.</i>
Colour reddish-brown. Articulations 2 or 3 times as long as broad	<i>P. rhunensis.</i>
28. Plant pale straw-coloured or brownish	<i>P. fibrillosa.</i>
Not so	29
29. Ramuli tapering at base and apex	<i>P. elongata.</i>
Not so	30
30. Plants tufted from the base	31
Having conspicuous main axis	32
31. Ramuli dichotomous	<i>P. fibrata.</i>
Ramuli alternate	<i>P. spinulosa.</i>
32. Axils of lower branches markedly obtuse	<i>P. elongata.</i>
Axils of lower branches acute	<i>P. violacea.</i>

I. ECORTICATE SPECIES.

A. Four primary pericentral siphons.

1. *P. INSIDIOSA* Crouan, Flor. Finist. 1867, p. 156 (non Grev.).

Grammita Richardsoni Crouan in Desmaz. exs. 1209, 1842 (non Hook.).

G. insidiosa Desmaz. exs. 1209 [corrected label].

P. havanensis var. *insidiosa* J. G. Ag. Spec. Alg. ii. 1863, p. 960.

Icones. Crouan, Flor. Finist. 1867, pl. 24. fig. 154. Bornet & Thuret, Recherch. sur la Fécond. des Florid., Ann. Sc. Nat. Bot., 5^e sér. vii. 1867, pl. 12. figs. 18–20. *Essiccat.* Crouan, Alg. mar. Finist. no. 293, 1852. Desmazières, exs. no. 1209 (with fig.), 1842. Lloyd, Alg. Ouest Fr. no. 296, 1854.

DESCRIPTION.—*Habit.* Occurring in tufts, branched from the base. Branching pseudo-dichotomous, ramuli alternate or unilateral. Diameter of the branches variable, attenuate upwards. *Siphons.* 4 pericentral and very small central. *Colour.* Greyish-brown, becoming black in drying. *Anatomy.* Articulations visible throughout the plant. Lower articulations and those of the ramuli once or twice as long as broad, those of the upper parts of main branches 3–4 times their breadth. Cell contents tending to adhere to inner wall of pericentral siphons, probably accounting for the greyish colour of the plant when fresh. *Attachment organ.* Plant attached to substratum by a number of rhizoids, each bearing a disc at the distal end. Rhizoids formed by lateral proliferation of pericentral siphons on creeping parts of lowest branches. *Reproductive organs.* Tetraspores borne in distorted ramuli. Antheridia cylindrical, obtuse at the apices. Cystocarps ovate, sessile on the ramuli.

P. insidiosa has not been described before from this country. It is not mentioned by Harvey (28), Batters (9), or De Toni (22). Agardh regards *P. insidiosa* as a simple form of *P. havanensis* (2. p. 960), but Thuret (54. p. 85) does not support this view. There appears to be sufficient difference both in habit and anatomical characters to confirm the view that *P. insidiosa* is a distinct species; moreover, its branches are much more variable in size than those of *P. havanensis*. *P. insidiosa* might be confused with some forms of *P. rhunensis*, but the antheridia of the former have longer stalks. Also the branches of *P. rhunensis* arise alternately and the articulations are shorter.

Habitat. Occurring on muddy rocks, large stones, and on other algæ at extreme low-water mark. Rare.

British Records. Yarmouth, Studland, Swanage, Weymouth (leg. A. D. Cotton, 1908), and Torquay.

Distribution in Europe. Occurring off the coast of N.W. France.

2. *P. MACROCARPA* Harv. in Mackay's "Flora Hibernica," iii. 1836, p. 206.

P. pulvinata Harv. Phyc. Brit. pl. 102. B, syn. 108 (excl. syn.).

P. sertularioides Holmes & Batters, Rev. List, 1892, p. 94.

References. Agardh (2) ii. p. 969 ; Batters (9) p. 79 ; Cotton (16) p. 138 ; De Toni (22) iv. p. 870 ; Hauck (31) p. 219.

Icones. Harvey, Phyc. Brit. l. c. *Exsiccator.* Crouan, Alg. mar. Finist. no. 288 (excl. syn.), 1852. Wyatt, Alg. Damnou. no. 215.

DESCRIPTION.—*Habit.* Occurring in roundish tufts, rarely more than an inch in height. Main branches showing marked tendency to pseudo-dichotomy, ramuli unilateral or alternate, generally backwardly directed. *Siphons.* 4 pericentral and small central. *Colour.* Dark reddish-brown. *Anatomy.* Length of articulations variable, 3–4 times as long as broad in the main branches, 2–3 times their breadth in the smaller branches, frequently not more than half their breadth in the ramuli. *Attachment organ.* Young plant attached to substratum by two rhizoids formed by longitudinal proliferation of pericentral siphons. Later, the siphons of procumbent branches form numerous rhizoids, each bearing a well-developed disc. The latter encircle angular fragments when the plant grows on a sandy substratum. *Reproductive organs.* Tetraspores borne in the ramuli, intercalary in development. Cystocarps stalked, urn-shaped, elongated at the apex with a contracted ostiole, very large in proportion to the diameter of the filament.

P. macrocarpa was wrongly united with *Hutchinsia pulvinata* Ag. and *Conferva pulvinata* Roth, Cat. ex Phyc. Brit. (28. p. 120), but rightly presented by Batters (9. p. 79). Bornet (11. p. 306) suggests that *P. macrocarpa* is a form of *P. sertularioides*, although he has kept them apart. *Hutchinsia pulvinata* Ag. has six pericentral siphons, and has been separated by Areschoug as *P. hemispherica* (11. p. 306).

Habitat. Occurring on rocks between the tide-levels and creeping in the sand. Common.

British Records. North Ronaldsay, Berwick, Cullercoats, Brighton, Isle of Wight, Studland, Swanage, Portland, Torbay, Plymouth, Fowey, Falmouth, Sennen Cove, Mount's Bay, Padstow, Ilfracombe, Anglesea, Hilbre Island, Ardrossan, Saltcoats, Bute, Port Stewart, Balbriggan, Milntown Malbay, and the Channel Islands.

Distribution in Europe. Atlantic and Mediterranean coasts.

3. *P. RHUNENSIS* Thuret, Études Phyc. 1878, p. 84.

Reference. Oltmanns (45) i. p. 600 *et seq.*

Icones. Thuret & Bornet, Études Phyc. 1878, pl. 41. Oltmanns, Morph. und Biol. der Algen, 1904, fig. 377.

DESCRIPTION.—*Habit.* Occurring in tufts, 8–10 cms. in length, branched from the base. Branches arising alternately, upper parts being clothed with

numerous ramuli. Filaments attenuate upwards, varying from .5–.05 mm. in diameter. *Siphons*. 4 pericentral round small central. *Colour*. Reddish-brown. *Anatomy*. Articulations visible throughout the plant; 2–3 times as long as broad in the middle parts of the main branches, diminishing to a length equal to their breadth in the ramuli, and shorter than their breadth near the attachment organ. Tips of branches clothed with dichotomising fibrillæ during the summer. *Attachment organ*. Young plant attached by rhizoids with discs at their apices, the rhizoids being formed by longitudinal proliferation of pericentral siphons. Later, rhizoids produced by pericentral siphons of procumbent branches. *Reproductive organs*. Tetraspores borne in swollen and distorted ramuli. Antheridia cylindrical, obtuse, rounded at their apices, borne on the dichotomising fibrillæ. Cystocarps very shortly stalked, almost sessile, ovate, with short ostiole which is frequently sinuous.

Habitat. Occurring on rocks and stones near low-water mark. Rare.

British Records. Plymouth, Trevone Bay, and Ilfracombe.

Distribution in Europe. In France on the inter-tidal roadway called Le Rhun, connecting the mainland at Saint-Vaast la Hougue with the little island of Tatihou.

4. *P. SPIRALIS* Batten, spec. nov.

Frondes rubiginose-fuscescentes, cæspitosæ, pollicares vel usque ad 25 mm. altæ, e filis repentibus ortæ, irregulariter divisæ, chartæ adhærentes. Rami inferiores repentibus substrato adfixi, copiose rhizoidiphori, articulis instructi diametro brevioribus, siphonibus rectis. Rami ascendentes et erecti articulis instructi diametro usque ad 3-plo longioribus et siphonibus valde sed regulariter contortis. Articuli quatuor siphonibus instructi, circa siphonem centralem dispositis, sectione transversali quadratum formantes, semper ecorticati. Tetrasporangia in ramulis non contortis, articulis iterum brevioribus. Antheridia et cystocarpia non visa.

Habitat ad saxa, in regione inferiori litorali, ad Durlston Head, Swanage, Britannicæ.

Legit auctor.

DESCRIPTION.—*Habit*. Occurring in small tufts rarely more than an inch in height. Branches either arising alternately or showing a marked tendency to a unilateral arrangement, the latter being accentuated in the parts bearing tetraspores. Ramuli often backwardly directed, though not as conspicuously as in *P. macrocarpa*. Substance gelatinous, adhering to paper. *Siphons*. 4 pericentral round large central. *Colour*. Brownish. *Anatomy*. Articulations no longer than their breadth in the procumbent parts of the plant, 3 times as long as broad in the upright branches, diminishing in the ramuli. Pericentral siphons parallel to the long axis of the filament in the lower parts of the plant and in the ramuli, but spirally

curved in the main branches. *Attachment organ.* Young plant attached at the base by two rhizoids formed by longitudinal proliferation of basal siphons. Later, numerous rhizoids are formed by lateral proliferation of procumbent branches, the siphons of which are parallel. *Reproductive organs.* Tetraspores are intercalary in development, and are borne in the ramuli. Antheridia and cystocarps have not yet been recorded.

The species somewhat resembles *P. macrocarpa* Harv. in outward appearance, but a slight torsion of the branches is visible to the naked eye, and the colour is much darker than in *P. macrocarpa* Harv. *P. spiralis* differs from *P. platyspira* Kütz. (37. xii. p. 63) in that the branching is not pseudo-dichotomous in the former species. The spiral twisting of the siphons is comparable to that of *P. havanensis* Kütz. (37. xiii. p. 72), but the branching and general habit of the plant are dissimilar. The large size of the central siphon makes it clear that the plant is not a young form of *P. urceolata* which is exhibiting a variation, and the length of the articulations bears out the view. *P. macrocarpa*, too, has a much smaller central siphon than *P. spiralis*.

Habitat. On rocks and groins near low-water mark.

British Records. Dorset at Durlston Head, Swanage, and between Sandbanks and the Haven.

5. *P. URCEOLATA* Grev. Flora Edinensis, 1824, p. 309.

P. formosa Suhr (not Harvey) in Flora, xiv. (1831), p. 709.

Grammita uncinata Bonnem. (not *P. uncinata* Kütz.) Ess. d'une class. des Hydro. loc., Journ. de Physique, xciv. 1822, p. 191.

P. denticulata Kütz. Tab. Phyc. xiii. 1863, p. 28, tab. 90 (*e-g*).

P. stricta Kütz. Tab. Phyc. xiii. 1863, p. 25, tab. 78 (*d-g*).

P. patens Kütz. Tab. Phyc. xiii. 1863, p. 29, tab. 91 (*c-e*).

Conferva urceolata Lightf. ex Dillw. p. 82, suppl. pl. G.

References. Agardh (2) ii. p. 970; De Toni (22) iv. p. 875; Hauck (31) p. 221; Falkenberg (24) pp. 150, 152.

Irones. Kütz. Tab. Phyc. l. c. Harvey, Phyc. Brit. 1846-51, pl. 167. syn. 106. *Exsiccator.* Desmazières, exsic. no. 1207, 1842. Lloyd, Alg. Ouest Fr. no. 174, 1854. Wyatt, Alg. Damnon. no. 133.

DESCRIPTION.—*Habit.* Occurring in tufts from 15-23 cms. long. Branching pseudo-dichotomous in the main branches, ramuli alternately branched and arising alternately, often flexed. *Siphons.* 4 pericentral round minute central. *Colour.* Deep red. *Anatomy.* Length of articulations 3-5 times their breadth in the principal branches, approximately equal to their breadth in the lower parts of the plant and rather shorter in the ramuli. *Attachment organ.* Main axis of young plant attached at the base by one or two rhizoids, the central siphons of procumbent branches producing rhizoids

later, which bear discs or branch-like structures at their apices. The contents of the rhizoid pass into the branches, but no wall is formed. *Reproductive organs.* Tetraspores borne in the upper parts of the ramuli, usually extending to the tip. Antheridia elongated, narrow, and stalked, borne on the tips of lateral ramuli. Cystocarps shortly stalked, elongated, borne on the upper branches and ramuli.

There seems to be no adequate reason for putting *P. formosa* Suhr into a separate species. J. G. Agardh, Sp. Alg. ii. p. 971, and Batters (9) p. 79 regard *P. formosa* Suhr as a variety of *P. urceolata* (Lightf.), and this appears to be the maximum amount of separation which is justifiable. *P. formosa* Suhr has longer articulations than *P. urceolata* (Lightf.), and is more gelatinous when young. *P. urceolata* (Lightf.) is usually considered to be an annual, appearing in summer, but specimens occur at Kew, collected by Mrs. Griffiths, in which the base of the branches are clothed with a few broken ramuli, large tufts occurring at the top. This is evidently due to the lower branches having existed through the winter, and then in spring thrown off tufts of fresh ramuli. The same phenomenon has been observed in specimens obtained from Plymouth. Specimens obtained from the Nothe Pools, Weymouth (leg. A. D. Cotton, 1908) were pale pink when fresh, but became very dark in drying. The plants were 6.5 cms. in height, and the articulations of the main branches rather shorter than is typical for the species.

Habitat. Occurring on rocks, limpet shells, and large algæ, particularly *Laminaria*, near low-water mark. Common.

British Records. Scotland, Northumberland, Durham, Yorkshire, Norfolk, Kent, Sussex, Hants, Dorset, Devon, Cornwall, Cheshire, Isle of Man, Wales, Ireland, and the Channel Islands.

Distribution in Europe. Atlantic shores of Northern Europe.

B. More than four primary pericentral siphons.

1. *P. ATRO-RUBESCENS* Grev. Flora Edinensis. 1824, p. 308.

P. Agardhiana Grev. Scot. Crypt. Flora, iv. 1826, p. 210.

Conferva atro-rubescens Dillw. Brit. Conf. 1809, pl. 70.

C. nigra Hudson, Flora Anglica, 1798, p. 595.

P. discolor (Ag.) Kütz. Spec. Alg. 1849, p. 825.

P. nigra Batt. Catal. Brit. Mar. Alg. 1902, p. 81.

References. Agardh (2) ii. p. 1035 *et seq.*; De Toni (22) iv. p. 938; Hauck (31) p. 243.

Icones. Greville, Scot. Crypt. Flora, l. c. Dillwyn, Brit. Conf. l. c. Harvey, Phyc. Brit. pl. 172. syn. 125. Kützinger, Tab. Phyc. xiii. 1863, p. 26, tab. 82 (*d-g*). *Exsiccata.* Desmazières, exs. no. 1205, 1842. Crouan, Alg. mar. Finist. no. 309, 1852. Lloyd, Alg. Ouest Fr. no. 16, 1854. Wyatt, Alg. Damnon. no. 134.

DESCRIPTION.—*Habit.* Plants attaining a length of 30 cms., main axis often pseudo-dichotomously branched, smaller branches arising alternately, the whole being clothed with short spine-like ramuli. Small branches and ramuli tapering at the base and apex. *Siphons.* 8–14 pericentral and large central. *Colour.* Dark red when young, later becoming almost black. *Anatomy.* Articulations no longer than their breadth in the procumbent parts, 2–3 times as long as broad in the principal parts of the main branches, becoming gradually shorter near the apices. Pericentral siphons spirally curved in the main branches, less so in the smaller branches and ramuli, and parallel to the long axis of the branch in the procumbent parts. *Attachment organ.* In the young plant the lowest articulations have fewer pericentral siphons, and two or more of the latter are elongated into attachment rhizoids with discs at their extremities. After branching has occurred, rhizoids are developed from the procumbent parts of the lowest branches by proliferation of pericentral siphons. *Reproductive organs.* Tetraspores are intercalary in origin and developed in swollen ramuli. Cystocarps sessile or very slightly stalked and broadly ovate with a large open ostiole.

Habitat. Occurring on rocks, stones, and shells such as *Pecten maximus*, only exposed at low tide or obtained by dredging. Not common.

British Records. Orkney, Elgin, Aberdeen, Kincardine, Forfar, Fife, Edinburgh, Haddington, Berwick, Northumberland, Yorkshire, Norfolk, Essex, Kent, Sussex, Hants, Dorset, Devon, Cornwall, Bute, Ireland, and the Channel Islands.

Distribution in Europe. Atlantic coasts.

2. *P. FASTIGIATA* Grev. Flora Edinensis, 1824, p. 308.

Hutchinsia fastigiata C. A. Agardh, Syn. Alg. Scan. 1817, p. 53.

Ceramium fastigiatum Roth, Catalecta Bot. iii. 1806, p. 157.

Conferva polymorpha Linn. Syst. Nat. ii. 1765, p. 721.

Grammita fastigiata Bonnem. Ess. d'une class. des Hydro. loc. 1822, p. 45.

References. Agardh (2) ii. pp. 67 & 1029; De Toni (22) iv. p. 946; Falkenberg (23) p. 149; Tobler-Wolff (55).

Icones. Harvey, Phyc. Brit. pl. 299. syn. 127. Klützing, Tab. Phyc. xiii. 1863, p. 14, tab. 44 (a–d). *Exsiccata.* Desmazières, exs. no. 254, 1842. Crouan, Alg. mar. Finist. no. 307, 1852. Lloyd, Alg. Ouest Fr. no. 104, 1854. Wyatt, Alg. Damnon. no. 177.

DESCRIPTION.—*Habit.* Plants about 7.5 cms. in height, perennial, forming dense tufts. Branching dichotomous, apices outspread. *Siphons.* 12–24 pericentral and large central. *Colour.* Dark reddish-brown. *Anatomy.* Articulations shorter than their breadth; contents of central siphon conspicuously dark in colour, shut down into a flattened mass by thickening of the wall in upper and lower parts of the siphon. *Attachment organ.*

Rhizoids, produced by the elongation of pericentral siphons, penetrate into the tissues of the host, the latter being almost invariably *Ascophyllum nodosum*. Procumbent branches creep along the thallus of the host, and send out rhizoids at intervals. Tips of the rhizoids swollen, with thin walls, closely applied to cells of the host which have become dark in colour. Dark cells also present in the thallus of the host in the area surrounding the path taken by the invading rhizoid. *Reproductive organs.* Tetraspores are borne in swollen terminal branches. Antheridia bright yellow in colour, borne in winter and spring in elongated clusters at the tips of the branches. Cystocarps sessile, egg-shaped, replacing one of the apical dichotomous branches.

The protoplasmic connections between the central and pericentral siphons are very well seen in young plants of *P. fastigiata*, although the maintenance of the connection between these siphons throughout the life of the plant has been the subject of much debate. Harvey Gibson (27. p. 129 *et seq.*) has shown that the continuity of the protoplasm is not maintained in the older parts of the plant. The pit between the siphons becomes closed by the development of a cellulose plate, and, although fine granular striæ are visible, maceration shows that these are due to a fringe of fine threads which arise along the margin of the plate. They are quite independent of the protoplasmic contents of the canal.

Polysiphonia usually attacks its host in the depression from which a new shoot will arise. This crevice forms a suitable substratum for the early stages of development of the plant, and rhizoids are soon produced by the elongation of single siphons which penetrate into the tissue of the host-plant. Tobler-Wolff (55) suggests that the reason *P. fastigiata* selects *Ascophyllum* as its host is the fact that the outer cells occur in chains in this species, and penetration is thus made more simple. This, however, seems an inadequate explanation of the phenomenon, as the epiphyte has been recorded on other Fuci. The cells which have been attacked by the *Polysiphonia* are dark in colour, and do not re-act when treated with vanillin in concentrated HCl. The ordinary *Ascophyllum* cells contain food-store, which turns red in the presence of the vanillin, and the failure of the dark cells to react shows that food must have been extracted from them.

Tobler-Wolff (55) in describing the dark cells says:—"Es war von vornherein anzunehmen, dass eine so tief eingreifende Befestigung—die wohl in dieser Weise für keinen anderen Fall bekannt ist—nicht ohne Schädigung des Substrates vor sich gehen kann. Tatsächlich sieht man auf entsprechenden Schnitten in der unmittelbaren Umgebung der Rhizoiden fast immer eine Anzahl Zellen mit auffallendem Inhalt. Er ist glasig, von einem rötlichen Braun, das von dem hellen gelbbraunen Ton der anderen Zellen stark absticht. Zudem sind diese Zellen meist aus dem Gewebeverband losgelöst; sie sind abgestorben."

It is evident that the *Polysiphonia* has obtained food from the dark cells, and also there seems no other explanation of the need for the swollen thin-walled tip of the rhizoid, which applies itself so closely to the host cells (see page 277 *et seq.*).

It is not absolutely necessary for the life of the *Polysiphonia* that it should be fixed to any host, but on the rare occasions when it occurs on a rocky substratum its vegetative growth is less perfect, although external conditions are similar with respect to depth and general environment. This shows that a direct advantage is gained by an epiphytic habit, and the statement is amplified by an examination of the anatomy.

There is frequently a slight local modification of the cells of the host in the immediate vicinity of the penetration of the *Polysiphonia*. Sometimes a little swelling occurs, and very frequently the cortical cells are displaced so that they no longer occur in chains.

Habitat. Occurring chiefly on *Ascophyllum nodosum*, but occasionally found on *Fucus serratus* and *Fucus vesiculosus*. It rarely occurs on a rocky substratum. Common.

British Records. Very common on the shores of the British Islands wherever its host-plant, *Ascophyllum nodosum*, grows.

Distribution in Europe. Atlantic shores and Baltic Sea.

3. *P. furcellata* Hook. in Smith's English Flora, v. 1833, p. 332.

P. forcipata J. G. Ag. Alg. Med. 1842, p. 127.

Reference. Agardh (2) ii. p. 1025.

Icones. Harvey, Phyc. Brit. pl. 7. syn. 126. Johnstone & Croall, Nat. print. Brit. Seaweeds, pl. 22½. 1859. Kützinger, Tab. Phyc. xiii. p. 25, tab. 79, 1863. *Exsiccata.* Crouan, Alg. mar. Finist. no. 306, 1852. Lloyd, Alg. Ouest Fr. no. 230, 1854.

DESCRIPTION.—Habit. Plants 12–14 cms. in length, with a well-marked central axis and numerous lateral branches. Main branches arising alternately with very wide axils, smaller branches and ramuli showing marked pseudo-dichotomy, apices being eventually clad with clusters of fibrillæ. *Siphons.* 8 or 9 pericentral round small central. *Colour.* Brick-red when fresh, becoming much darker in the herbarium. *Anatomy.* Length of articulations 3–5 times their breadth in the main branches, diminishing in the smaller branches, and only equal to their breadth in the ramuli. *Reproductive organs.* Tetraspores are intercalary in development, and are borne in distorted ramuli. Cystocarps are ovate and sessile. Antheridia are borne in clusters at the tips of the ramuli.

P. ceramiaeformis Croton appears to have been assigned to a young form of *P. furcellata*, which is perhaps nearest to *P. furcellata* *a. forcipata* Ag. (2) ii. p. 1025. The articulations in this form are shorter than those of *P. furcellata*, and the siphons number eleven or twelve.

Habitat. Usually recorded either dredged or floating. Rare.

British Records. Norfolk coast (*vide* Geldart), Studland, Weymouth, Sidmouth, Torquay, Plymouth, Falmouth, Carrickfergus, Roundstone, and Jersey.

Distribution in Europe. Atlantic shores of France.

4. *P. OBSCURA* J. G. Ag. Alg. Med. 1842, p. 123.

Conferva intertexta Roth, Catalecta Bot. i. 1797, p. 188, tab. 2. fig. 5 ;
ii. 1800, p. 214.

P. adunca Kütz. Tab. Phyc. xiii. 1863, p. 13, tab. 40 (*c-e*).

P. reptabunda Kütz. *l. c.* xiii. 1863, p. 12, tab. 34 (*d-g*).

References. Agardh (2) ii. p. 943 ; Falkenberg (24) p. 500 ; Hauck (31) p. 244.

Icones. Harvey, Phyc. Brit. pl. 102. A. syn. 120. Kütz. Tab. Phyc. *l. c.*

DESCRIPTION.—*Habit.* Forming low tufts 1–3 cms. in height, branched from the base, branches being monopodial in origin. Not adhering to paper. *Siphons.* 12–18 pericentral and a large central one. *Colour.* Dark brown. *Anatomy.* Articulations as long as broad, or sometimes rather shorter. *Attachment organ.* Rhizoids developed in abundance by lateral proliferation of pericentral siphons. Well-developed discs formed at the extremities when a firm substratum is encountered. *Reproductive organs.* Tetraspores are intercalary in development ; formed spirally in much-branched filaments, only one group of tetraspores occurring in an articulation. Antheridia and cystocarps unknown.

P. obscura is distinguishable as having the most diminutive habit among British species with so large a number of siphons. The attachment organ is very similar to that of *P. macrocarpa* when the latter creeps in the sand.

Habitat. Occurring in tufts on sheltered rocks, on the attachment organs of Fuci, and on smaller algæ. Very rare.

British Records. Weymouth, Ladrán Bay, Sidmouth, Mount Edgcumbe, Penzance, Pridmouth, Jersey, and Guernsey.

Distribution in Europe. Coast of Spain, Adriatic Sea.

5. *P. OPACA* Zanard. Syn. Alg. in Mari Adriat. 1842, p. 63.

Hutchinsia opaca C. A. Ag. Syn. Alg. Scandin. 1817, p. 148.

P. repens Kütz. Tab. Phyc. xiii. 1863, p. 13, tab. 39 (*d-f*).

P. virens Kütz. *l. c.* p. 14, tab. 41 (*a-c*).

P. condensata Kütz. *l. c.* p. 14, tab. 41 (*d-g*).

P. erythrocoma Kütz. *l. c.* p. 14, tab. 43 (*a, b*).

P. fasciculata Kütz. *l. c.* p. 15, tab. 44 (*d, e*).

P. umbellifera Kütz. *l. c.* p. 15, tab. 45 (*a, b*).

P. ophiocarpa Kütz. *l. c.* p. 15, tab. 47 (*c-f*).

P. tripinnata Kütz. (non Ag.) *l. c.* p. 16, tab. 48 (*a, b*).

P. macrocephala Zanard. ex Kütz. *op. cit.* xiv. 1864, p. 19, tab. 53 (*e-g*).

P. spiculifera Zanard. ex Kütz. *op. cit.* xiv. 1864, p. 17, tab. 49 (*a-c*).

References. Agardh (2) ii. p. 1055 ; De Toni (22) iv. p. 942 ; Falkenberg (24) p. 120 *et seq.* ; Hauck (31) p. 246.

Icones. Kützing, Tab. Phyc. xiii. & xiv. l. c.

DESCRIPTION.—*Habit.* Plants from 1–9 cms. high. Branching alternate or pseudo-dichotomous in the principal branches, irregularly alternate in the smaller branches and ramuli, the ramuli being short and spine-like, and closely set on the shorter branches. *Siphons.* 20 or more pericentral round central one of diameter roughly equal to the radius of the filament. *Colour.* Brownish, becoming black in drying. *Anatomy.* Articulations usually about as long as broad, sometimes attaining a length of $1\frac{1}{2}$ times their breadth. During summer, tips of branches and ramuli clothed with colourless multi-cellular dichotomising filaments. *Attachment organ.* Young plant attached at the base by rhizoids developed longitudinally from the pericentral siphons. Procumbent branches produce new rhizoids later, each having a disc at its extremity. *Reproductive organs.* Tetraspores intercalary in development, not always occupying successive articulations of the ramulus. Antheridia occurring in tufts on the terminal dichotomising fibrillæ, replacing some of the branches. Cystocarps ovate in form, sessile on the ramuli.

Habitat. Occurring between the tide-marks. Rare.

British Records. Petit Port, Guernsey.

Distribution in Europe. Adriatic Sea.

6. *P. RICHARDSONI* Hook. in Smith's English Flora, v. 1833, p. 333.

Reference. De Toni (22) iv. p. 920.

Icones. Harvey, Phyc. Brit. pl. 10. syn. 111.

DESCRIPTION.—*Habit.* Plants attaining a length of 8–10 cms. Main axis much branched and zigzag in form, with lateral branches arising at an angle of nearly 90°. Ramuli slender and like the branches, alternate in origin. *Siphons.* 5 round a smaller central. *Colour.* Reddish-brown, becoming darker in drying. *Anatomy.* Articulations three or four times as long as broad in the middle parts of the plant, where the pericentral siphons are spirally twisted. Articulations shorter and siphons parallel to the long axis in the upper parts. *Attachment organ.* Examination of Richardson's specimen in the Herbarium Hookerianum at Kew shows a disc-like attachment organ comparable to that of *P. elongella*. *Reproductive organs.* Cystocarps borne near the tips of the branches, globose and sessile with a wide ostiole.

De Toni (22. iv. p. 920) suggests the possibility of *P. Richardsoni* Hook. being synonymous with *P. rhunensis* Thur., but this is not practical, owing to the anatomy of the plant, the total difference of attachment organ, and the difference of habit. *P. Richardsoni* Hook. is probably near to *P. collabens*

Ag. (2) ii. p. 1022, to which it bears considerable resemblance anatomically. The specimen in the Herbarium Hookerianum at the Royal Botanic Gardens, Kew, was collected by Richardson. Harvey (28. p. 111) noticed the striking similarity between the branching of *P. Richardsoni* Hook. and *P. elongella* Harv., but remarks that there is no resemblance to any other character, evidently having omitted to examine the attachment organ.

Habitat. Detailed habitat unknown.

British Records. Colvend, Kirkcudbright (Richardson).

Distribution in Europe. Nil.

7. *P. SIMULANS* Harv. Man. Brit. Mar. Alg. ed. ii. 1849, p. 89.

P. spinulosa Harv. Man. Brit. Mar. Alg. ed. i. 1841, p. 87 (non Grev.).

P. divergens γ. *Grevilleana* Kütz. Sp. Alg. 1849, p. 822.

References. Agardh (2) ii. p. 1051; De Toni (22) iv. p. 935.

Icones. Harvey, Phyc. Brit. pl. 278. syn. 121. *Exsiccator.* Crouan, Alg. mar. Finist. no. 304, 1852. Lloyd, Alg. Ouest Fr. no. 279, 1854.

DESCRIPTION.—*Habit.* Plants tufted from the base; branches arising alternately, sparsely clothed with irregularly pinnate ramuli, the latter tapering sharply at the apex. *Siphons.* 12 pericentral round a central one of diameter equal to about $\frac{1}{3}$ – $\frac{2}{3}$ times the radius of the whole filament. *Colour.* Reddish-brown. *Anatomy.* Articulations about one and a half times as long as broad in the main branches, but shorter than their breadth in the ramuli and at the extreme base of the plant. *Attachment organ.* Numerous rhizoids are developed by the proliferation of pericentral siphons, each rhizoid bearing a well-formed disc at its distal end. The main branches creep along the substratum for a short distance, producing an aggregation of discs. *Reproductive organs.* Tetraspores intercalary in development, borne in distorted ramuli. Cystocarps sessile, ovate in form, borne on the smaller branches.

P. simulans is rigid when fresh, but adheres to paper after immersion in fresh water. It is much darker in colour than *P. subulifera*. Should any confusion occur between some forms of this species and *P. nigrescens*, a transverse section at the extreme base of one of the main branches is often a decisive factor in determination. *P. simulans* is ecorticate throughout, while at the base of *P. nigrescens* there is frequently a row of corticating cells. The serrate appearance due to the remains of old branches so frequently to be observed in *P. nigrescens* does not occur in *P. simulans*. The aggregation of attachment discs is similar in the two species.

Habitat. Occurring near low-water mark. Most often found on thin-bedded and eroded schists. Rare.

British Records. Skail, Studland, Swanage, Torbay, Plymouth, Mount Edgcumbe, Falmouth, Mount's Bay, Arran, Cumbrae, Valentia, and Kerry.

Distribution in Europe. Unknown.

8. *P. SUBULIFERA* (Ag.) Harv. in Hooker's Journal of Botany, vol. i. 1834, p. 301.

Hutchinsia subulifera C. A. Ag. in Bot. Zeit. 1827, p. 638.

P. armata J. G. Ag. Alg. Mar. Medit. et Adriat. 1842, p. 810.

P. pantophlœa Kütz. Tab. Phyc. xiv. 1864, p. 5, tab. 13 (a-c).

P. ramellosa Kütz. l. c. p. 9, tab. 26 (a-b).

References.—Agardh (2) ii. p. 1052; Cotton (16) p. 139; Crouan (17) ii. p. 311; De Toni (22) iv. p. 936; Harvey (28) pl. 228.; Kützing (37) iv. p. 936.

Icones. Harvey, Phyc. Brit. pl. 227. syn. 124; Kützing, Tab. Phyc. l. c. *Exsiccate*. Crouan, Alg. mar. Finist. no. 311, 1852. Lloyd, Ouest Fr. no. 278, 1854. Wyatt, Alg. Damnon. no. 178.

DESCRIPTION.—*Habit*. The species is an annual, appearing in summer and growing to a length of 8 inches under favourable conditions. Occurring in tufts, branched from the base and beset with alternate short spine-like ramuli, the tips clothed with clusters of almost colourless filaments when the plant is young. *Siphons*. 12–13 pericentral round a central one of diameter equal to about $\frac{1}{4}$ of the radius of the filament. *Colour*. Deep red when fresh, but becoming dark when gathered. *Anatomy*. Articulations varying in length from 2–3 times their breadth in the main branches to a length equal to their breadth in the smaller branches and ramuli. *Attachment organ*. Attached by rhizoids developed from pericentral siphons of procumbent branches. *Reproductive organs*. Tetraspores borne in distorted ramuli. Antheridia and cystocarps unknown.

The species is rigid when fresh, but soon becomes flaccid when gathered. It is usually only obtainable by dredging in from 4–10 fathoms of water, and examination of *complete* attachment organs proved impossible. It is a characteristic feature that the ramuli are short and spine-like, comparable to those of *P. fruticulosa*, from which it differs in the ecorticate form of the main axis. From *P. simulans* it is distinguished by larger size and lighter colour and difference in habitat, as it is rarely, if ever, found in the tide-pools at low water.

Habitat. Occurring in deep water, generally on Nullipore banks. Recorded from Jersey attached to *Rytiphlœa pinastroides* and *Polyides rotundus*, and from Roundstone (Cotton, Sept. 1911) on the *Lithothamnion* banks.

British Records. Weymouth, Torbay, Lamlash, Arran, Belfast, Carrickfergus, Roundstone Bay, Jersey, and Guernsey. Very rare.

Distribution in Europe. Adriatic Sea and coast of France.

II. CORTICATE SPECIES.

A. Four primary pericentral siphons.

1. *P. ELONGATA* (Huds.) Harv. in Smith's Engl. Flora, v. 1833, p. 333.
P. Ruchingeri Kütz. Tab. Phyc. xiv. 1864, p. 2, tab. 6 (*a-d*).
Hutchinsia strictoides Lyngb. Tent. Hydrophyt. Danicæ, 1819, p. 114.
P. trichodes Kütz. Tab. Phyc. xiv. 1864, p. 4, tab. 10 (*e-g*).
P. robusta Kütz. l. c. p. 4, tab. 11 (*a-c*).
P. stenocarpa Kütz. l. c. tab. 11 (*d-f*).
P. arborescens Kütz. l. c. p. 4, tab. 12 (*a-c*).
P. chalarophlora Kütz. l. c. p. 5, tab. 12 (*d-f*).
P. macroclonia Kütz. l. c. p. 5, tab. 13 (*d, e*).
P. rosea Grev. Fl. Edin. 1824, p. 310.
P. clavigera Kütz. l. c. p. 5, tab. 14 (*a-d*).
Hutchinsia elongata C. A. Ag. Syn. Alg. Scand. 1817, p. 54.
Ceramium elongatum Grev. Fl. Edin. 1824, p. 310.
Ceramium brachygonium Lyngb. Tent. Hydr. Dan. p. 118.
Conferva elongata Huds. Fl. Angl. ed. II. ii. 1778, p. 599.

References. Agardh (2) ii. p. 1004; De Toni (22) iv. p. 903; Falkenberg (24) p. 126 *et seq.*; Hauck (31) p. 227 *et seq.*

Icones. Harvey, Phyc. Brit. pls. 292 & 293. syn. 114. Kütz. Tab. Phyc. xiv. l. c. *Exsiccator.* Desmazières, exs. no. 1210, 1842. Crouan, Alg. mar. Finist. no. 301, 1852. Lloyd, Alg. Ouest Fr. nos. 55 & 305, 1854. Wyatt, Alg. Damnon. no. 40.

DESCRIPTION.—*Habit.* Plants usually solitary, 15–30 cms. long. Branches naked during the winter, clothed in spring with dense mass of ramuli. Branching alternate with sometimes a tendency to pseudo-dichotomy. Ramuli attenuate at base and apex. Main branches cartilaginous in texture, ramuli gelatinous. *Siphons.* 4 primary pericentral, alternating with which on the outside are 4 secondary. Surrounding these in the older parts eight tertiary siphons occur, bounded by a zone of corticating cells. *Colour.* Reddish-brown, very dark in the older parts; ramuli crimson. *Anatomy.* Articulations obscured in the older parts of the main axis by the dense band of peripheral corticating cells. In the smaller branches and ramuli articulations $1\frac{1}{2}$ to twice as long as broad. Protoplasmic continuity maintained throughout the thallus, fibrillæ passing through pits in the contiguous walls. *Attachment organ.* Base of main axis expanding into a disc formed by the activity of the siphons and corticating cells. Each of the cells and siphons at the base becomes elongated into a thick-walled rhizoid, the extreme base of which flattens out and attaches itself to the substratum. *Reproductive organs.* Tetraspores borne in lateral and terminal ramuli, which are swollen and distorted. Cystocarps borne on small branches, sessile or very slightly stalked, ovate in form but tending to be elongated.

The fact that the ramuli are attenuate at the base and apex is one of the distinguishing features of the species. *P. elongata* has been described as being either biennial or perennial, but close observation of individual plants has shown that it is perennial. According to Falkenberg (24. p. 126), the older plants may show a secondary development in which the cavities of the siphons become filled with small cells, comparable to those forming the cortication, although the wall of the original siphon is still visible. The attachment organ is one of the most elaborate found in the genus. Its development can doubtless be correlated with the corticate anatomy of the plant and its solitary habit. There are no procumbent branches present which can aid in the attachment, but the large number of siphons and corticating cells make it possible to develop a strong organ of attachment from the main axis alone. At the extreme base the corticating cells spread out in a more or less horizontal direction, so giving an increased surface for the development of rhizoids. In the greater part of the large expanded disc the walls of the rhizoids cohere mechanically, forming a pseudo-tissue (see p. 279 *et seq.*).

Habitat. Attached to stones and shells in pools and muddy bays between the tide-levels and in from 5-10 fathoms of water. Common.

British Records. Scotland, Northumberland, Durham, Yorkshire, Norfolk, Essex, Kent, Sussex, Hants, Dorset, Devon, Cornwall, Hilbre Island, Wales, Ireland, and Jersey.

Distribution in Europe. Atlantic and Mediterranean shores.

2. *P. ELONGELLA* Harv. in Smith's Engl. Flora, v. 1833, p. 334.

P. lophuroides Kütz. Tab. Phyc. xiii. 1863, p. 28, tab. 91 (a-b).

References. Agardh (2) ii., iii. p. 1002; De Toni (22) iv. p. 910; Hauck (31) p. 228.

Icones. Kütz. Tab. Phyc. xiii. 1863, tab. 91 (a-b). Harvey, Phyc. Brit. pl. 146. syn. 113. *Exsiccata.* Wyatt, Alg. Damnon. no. 84.

DESCRIPTION.—*Habit.* Plants as much as 13 cms. in height, usually solitary. Branching pseudo-dichotomous with wide angle of divergence, in the main branches, alternate in the smaller branches, which are densely clothed with ramuli during the spring and summer. Upper parts gelatinous in substance, basal parts cartilaginous. *Siphons.* 4 primary pericentral, alternating with which 4 secondary occur bounded by a band of corticating cells. *Colour.* Bright red in the ramuli, darker in the lower parts of the plant. *Anatomy.* Articulations rather shorter than their breadth at the base, about equal to their breadth in the main branches, and in the ramuli very short near the apices, increasing in length proximally. *Attachment organ.* Very similar in form to that of *P. elongata*, the siphons and corticating cells elongating longitudinally into thick-walled rhizoids which cohere mechanically with each other, forming a pseudo-tissue. *Reproductive organs.* Tetraspores

intercalary in development, borne in the tips of the branches and ramuli. Cystocarps large, stalked, ovate in form, with a tendency to elongate near the ostiole.

P. elongella often resembles *P. elongata*, but may be distinguished by the visibility of the articulations in all parts of the plant except the extreme base, cortication being less well developed in the former species. Also, the ramuli of *P. elongella* are not attenuate at the base as in *P. elongata*. According to Harvey (*l. c.* p. 113), Hauck (*l. c.* p. 228), and De Toni (*l. c.* p. 910), there are 4 pericentral siphons in each articulation, surrounded by a band of "cellules." It is evident, however, that 4 secondary siphons alternate on the outside with the 4 primary ones, before the corticating cells begin, these siphons differing from the cells in the fact that they occupy the whole length of an articulation.

Habitat. On rocks, stones, and smaller algæ near low-water mark and at greater depth. Rare, though widely distributed.

British Records. Kirkwall Bay, Peterhead, Elie, Brighton, Bognor, Isle of Wight, Swanage, Weymouth, Sidmouth, Torbay, Plymouth, Torpoint, Talland Bay, Falmouth, Padstow, Anglesea, Isle of Man, Saltcoats, Seamill, Ardrossan, Arran, Cumbræ, Kinn, Larne, Belfast Lough, Malahide, Howth, Killiney, Bantry, and Jersey.

Distribution in Europe. Coast of France and Adriatic Sea.

3. *P. FIBRATA* Harv. in Smith's Engl. Flora, v. 1833, p. 329.

Hutchinsia allochroa β . *fibrata* C. A. Ag. Syst. Alg. 1824, p. 154.

Grammita decipiens Bonnem. Hydroph. loc. 1822, p. 37.

References. Agardh (2) ii. p. 965; De Toni (22) iv. p. 893.

Icones. Harvey, Phyc. Brit. 1846-51, pl. 208. syn. 109. *Ersiccatæ*. Crouan, Alg. mar. Finist. no. 294, 1852. Lloyd, Alg. Ouest Fr. no. 193, 1854. Wyatt, Alg. Damnon. no. 39.

DESCRIPTION.—*Habit.* Occurring in tufts 20-23 cms. in length. Branching either alternate or pseudo-dichotomous, main branches being clothed with numerous ramuli, frequently bearing delicate fibrillæ at their tips. *Siphons.* 4 pericentral round a minute central one, a row of corticating cells frequently occurring at the extreme base. *Colour.* Red when fresh, become very dark on drying. *Anatomy.* Articulations variable in length, as much as eight times their breadth in the main branches, becoming shorter in the upper parts and scarcely twice as long as broad in the ramuli. Filaments slightly swollen at the junction of the articulations with each other. *Attachment organ.* Young plant attached by two or more rhizoids developed by longitudinal proliferation of pericentral siphons; other rhizoids occur later on the main axis and on procumbent branches, being formed by lateral proliferation of the siphons. A tendency to deep lobing of the expanded portion of the rhizoid frequently visible. *Reproductive organs.* Tetraspores intercalary in development, borne in distorted ramuli. Antheridia elongated

in form, and borne on apical fibrillæ at the tips of branches. Cystocarps stalked, ovate, with large open ostiole, borne on upper parts of branches and ramuli.

P. fibrata is usually darker in colour than *P. urceolata*, and it may also be distinguished from that species by its gelatinous nature. According to a note by Moore on a specimen from the Antrim coast preserved in the Herbarium of the Royal Botanic Gardens, Kew, the arrangement of the siphons is frequently spiral in this species. Material obtained from Torquay in April 1920 exhibited this phenomenon, the amount of twist being about equal to that which is typical for *P. atro-rubescens*.

Habitat. On rocks, stones, and shells at extreme low-water mark. Frequent.

British Records. Scotland, Northumberland, Kent, Sussex, Hants, Dorset, Devon, Cornwall, Hilbre Island, Wales, Isle of Man, Ireland, and the Channel Islands.

Distribution in Europe. Atlantic shores of Europe.

4. *P. FIBRILLOSA* Grev. in Smith's Engl. Flora, v. 1833, p. 334.

Hutchinsia fibrillosa C. A. Ag. Sp. Alg. vol. ii. 1828, p. 78.

H. lubrica C. A. Ag. l. c. p. 94.

P. lasiotricha Kütz. Tab. Phyc. xiii. 1863, p. 23, tab. 72 (e-h).

References. Agardh (2) ii. p. 991; De Toni (22) p. 919; Hauck (31) p. 230.

Icones. Harvey, Phyc. Brit. pl. 302. syn. 117. Kützting, Tab. Phyc. xiii. l. c. *Exsiccatæ.* Crouan, Alg. mar. Finist. no. 296, 1852. Lloyd, Alg. Ouest Fr. no. 136, 1854. Wyatt, Alg. Damnon. no. 136.

DESCRIPTION.—*Habit.* Plants solitary, as much as 15 cms. in length. Branching alternate, lowest ones longer than the upper, giving conical appearance. Branches clothed with numerous ramuli; substance cartilaginous except in the smaller branches and ramuli, where it is gelatinous. *Siphons.* 4 primary pericentral, with which the four secondary alternate on the outside, the diameter of the central one being about $\frac{1}{3}$ the radius of the filament. A band of corticating cells present at the base. *Colour.* Brownish or straw-coloured when growing in sunny pools, darker in deeper water. *Anatomy.* Articulations obscured in the lower parts of the plant; from $1\frac{1}{2}$ to twice as long as broad in the smaller branches and ramuli, the tips of the latter being clothed during summer with multicellular dichotomous hairs. *Attachment organ.* Plant attached by an expanded disc of the same type as *P. elongata*. Length of the rhizoids very variable when the plant is epiphytic, e.g. on *Rytiphloea pinastroides* Ag., the outer ones being longer and enabling the attachment disc to grasp the thallus of the host. *Reproductive organs.* Tetraspores intercalary in development in swollen ramuli. Antheridia borne on filamentous hairs at the apices

of the ramuli. Cystocarps sessile, ovate in form, borne on the smaller branches.

Antheridia are not recorded by Harvey (*l. c.*), Agardh (*l. c.*), or De Toni (*l. c.*), but were observed in a specimen in the Batters collection in the Natural History Museum, South Kensington.

Habitat. Occurring on rocks, stones, and other algæ, such as *Rytiplœa pinastroides*, in clear sunny tide-pools and also in deep water. Rare, but occurring in considerable quantity at uncertain intervals.

British Records. Orkney Islands, Stonehaven, Earlsferry, Dunbar, Berwick, Whitley, Roker, Cromer, Brighton, Shoreham, Isle of Wight, Swanage, Weymouth, Seaton, Sidmouth, Torquay, Plymouth, Looe, Falmouth, Mount's Bay, St. Minver, Isle of Man, Anglesea, Saltcoats, Isles of Arran, Bute and Cumbræ, Loch Coil, Bangor (Co. Down), Howth, Bantry, Miltown Malbay, Roundstone, and the Channel Islands.

Distribution in Europe. Atlantic shores, Baltic and Mediterranean Seas.

5. *P. SPINULOSA* Grøv. Scottish Cryptogamic Flora, vol. ii. 1824, p. 90.

Reference. Agardh (2) ii. p. 999.

Icones. Greville, Scottish Crypt. Fl. ii. 1824, pl. 90. Harvey, Phyc. Brit. 1846-1851, pl. 320. syn. 110.

DESCRIPTION.—Habit. Plant about 5 cms. in height. Branched from the base, branches arising alternately, clothed with short spine-like ramuli, each bearing a cluster of dichotomising fibrillæ at the tip. *Siphons.* 4 primary pericentral, alternating with which are 4 secondary, bounded by a row of corticating cells. *Colour.* Dark red. *Anatomy.* Articulations visible throughout the plant, their length being about equal to their breadth. *Reproductive organs.* Cystocarps sessile and ovate in form, occurring on the branches and ramuli.

P. SPINULOSA var. β . MAJOR, J. G. Ag. Spec. Alg. ii. 1863, p. 999.

= *P. Carmichaeliana* Harv. in Smith's Engl. Flora, v. 1833, p. 328.

Reference. Harvey (28) pl. 319. syn. 116.

This variety occurs on *Desmarestia aculeata*, and has been recorded by Captain Carmichael from Appin, and records have also been made from Little Cumbræ and Skaill, although the plant is very rare. The growth is more lax than that of *P. spinulosa*. There is a central axis from which the branches arise, rather similar to that of *P. fibrillosa*, but the branching is more delicate. A wider band of corticating cells occurs than is present in *P. spinulosa*.

Habitat. Probably in tide-pools. Rare.

British Records. Appin, Argyll (Carmichael's spec. in Herb. Hook., Kew).

Distribution in Europe, Nil.

6. *P. VIOLACEA* HARV. Man. Brit. Alg. ed. i. 1841, p. 92.

P. subulata J. G. Ag. Spec. Alg. ii. 1863, p. 985 (nec Kütz.).

Hutchinsia violacea C. A. Ag. Syn. Alg. Scan. 1817, p. 54.

References. De Toni (22) iv. p. 900; Falkenberg (24) p. 115; Hauck (31) p. 225.

Icones. Harvey, Phyc. Brit. 1846-51, pl. 209. syn. 115. *Fascicata.* Wyatt, Alg. Damnon. no. 176.

DESCRIPTION.—Habit. Plants consisting of a main axis, conspicuous at the base, but soon becoming alternately branched, the branches being densely clothed with alternate ramuli. Length usually about 12-15 cms., occasionally attaining a length of 25 cms. *Siphons.* 4 primary pericentral alternating with 4 secondary, bounded on the outside by a band of corticating cells. *Colour.* Brownish-purple. *Anatomy.* Articulations obscured at the base by the corticating cells, 2 to 4 times as long as broad in the smaller branches and ramuli. *Attachment organ.* Young plant attached by 2 or 3 rhizoids developed by longitudinal proliferation of the pericentral siphons. Later, the siphons and external cells at the base all develop rhizoids, and form an attachment organ similar in type to that of *P. elongata*. *Reproductive organs.* Tetraspores borne in swollen ramuli. Cystocarps ovate, usually shortly stalked, with no elongation in the region of the ostiole.

There seems to have been confusion between *P. violacea* and *P. nigrescens*, although the anatomy is so dissimilar. The confusion was probably due to a variety of *P. nigrescens*, which was brighter and purple in colour with greater delicacy of ramification, being described as *P. violacea* by Harvey in Smith's English Flora (p. 332). The *P. violacea* Harv. has been ascertained by Agardh to be identical with the *P. violacea* of Continental authors, which has only four primary siphons.

P. subulata Ag. differs from *P. violacea* Harv. only in the degree of cortication, which seems insufficient ground for a specific distinction.

P. VIOLACEA var. *GRIFFITHSIANA*, var. nov.

P. Griffithsiana Harv. Manual, 1841, p. 91; Phyc. Brit. 1846-51, pl. 228. syn. 112.

Pyramidal in form, attaining a length of as much as 25 cms. Axis consisting in the lower parts of 4 primary siphons and 4 secondary arranged round a central siphon. In the upper parts the four secondary are absent. Occasionally a few small corticating cells are present at the extreme base of the plant. Branches arising alternately, clothed with numerous ramuli which are sometimes dichotomously branched.

P. VIOLACEA var. *TENUISSIMA* Hauck, Meeresalg. 1885, p. 227.

P. divaricata Kütz. Tab. Phyc. xiii. 1863, p. 26, tab. 84 (a-c) [*vide* Hauck].

Plants delicate with lax growth, corticate at the base. Articulations 4 to 8 times as long as broad, branching showing marked pseudo-dichotomy.

The various species of *Polysiphonia* exhibit such diversity of form dependent on the conditions under which they are growing that it seems unnecessary to create new species for these forms until they have been shown to possess some stability.

Habitat. Occurring on rocks, stones, and on other algæ such as *Chorda filum* near low-water mark. Rather rare.

British Records. Orkney Islands, Peterhead, Elie, Earlsferry, Berwick, Whitley, Roker, Kent, Sussex, Hants, Dorset, Devon, Cornwall, Carnarvon, Isle of Man, Arran, Bute, Cumbrae, Howth, Bantry, Ferriter's Cove, Roundstone, and the Channel Islands.

Distribution in Europe. Generally distributed over the coasts of Northern Europe.

B. More than four primary pericentral siphons.

1. *P. BRODLÆI* Grev. in Smith's Engl. Flora, v. 1833, p. 328.

Grammita Brodiaei Bonnem. Hydroph. loc. 1822, p. 31.

P. penicillata Kütz. Spec. Alg. 1849, p. 827.

P. polycarpa Kütz. Tab. Phyc. xiv. 1864, p. 1, tab. 2 (*e-g*).

P. callitricha Kütz. l. c. tab. 2 (*a-d*).

References. Agardh (2) ii. p. 993 ; De Toni (22) iv. p. 947 ; Hauck (31) p. 237.

Icones. Harvey, Phyc. Brit. 1846-51, pl. 195. syn. 118. Kützling, Tab. Phyc. l. c. *Ersiccata*. Wyatt, Alg. Damnon. no. 83.

DESCRIPTION.—*Habit.* Plants branched from the base, frequently showing a distinct main axis. Branching irregular or pseudo-dichotomous, densely clothed with tufted ramuli. Substance cartilaginous, but flaccid in the ramuli. *Siphons.* 6-8 primary pericentral siphons, alternating with which occur the same number of secondary siphons bounded by a band of corticating cells. *Colour.* Dark purplish-red, becoming much darker in drying. *Anatomy.* Articulations of the main axis and principal branches entirely obscured by the cortication ; articulations of the ramuli about as long as broad. *Attachment organ.* Young plant attached to the substratum by a number of rhizoids formed by the longitudinal proliferation of the siphons and by the elongation of the corticating cells, a certain amount of mechanical coherence resulting in the formation of a disc as in *P. elongata*, although the individual rhizoids are looser. Later, certain of the procumbent branches form rhizoids by the lateral elongation of the corticating cells, thus giving additional strength to the organ. The form of the attachment organ thus comes intermediate between the *P. nigrescens* and *P. elongata* types. *Reproductive organs.* Tetraspores intercalary in development, borne in swollen ramuli. Cystocarps ovate in form and shortly stalked, developed in large numbers on the ramuli.

P. Brodiaei Grev. differs anatomically from *P. Brodiaei* Aresch., the latter having as many as 16 siphons in the main thallus and 12 in the ramuli. The ramuli are very numerous, giving the plant a distinctive tufted appearance.

Habitat. Occurring near low-water mark and at greater depth on rocks, corallines, and shells. Flourishes where conditions are turbulent. Common. *British Records.* Orkney Islands, Forres, Peterhead, Arbroath, Elie, Earlsferry, Dunbar, Berwick, Alnmouth, Whitley, Folkestone, Brighton, Isle of Wight, Swanage, Weymouth, Sidmouth, Torbay, Plymouth, Torpoint, Falmouth, Penzance, Isle of Man, Portincross, Arran, Cumbræ, Bute, South and West coasts of Ireland, and the Channel Islands.

Distribution in Europe. Atlantic shores of Europe as far south as France.

2. *P. FÆTIDISSIMA* Cocks, Alg. Fasc. Coll. Brit. Seaweeds, 1855, no. xxix [nomen]. "

P. stuposa Zanard. ex Kützing, Tab. Phyc. xiv. 1864, p. 18 (diagnosis); Ralfs in Penzance Nat. Hist. Soc. Trans. 1884, p. 325 [nomen].

References. De Toni (22) iv. p. 924; Hauck (31) p. 240 *et seq.*; Bornet (10) p. 154 [314].

Icones. Kützing, Tab. Phyc. xiv. 1864, p. 18, tab. 49 (*d-g*). *Exsiccata.* Cocks, Alg. Fasc. Coll. Brit. Seaweeds, 1855, no. xxix.

DESCRIPTION.—*Habit.* Occurring in tufts from 3–10 cms. in length. Branching alternate or pseudo-dichotomous, branches being clothed with numerous ramuli, especially in the upper parts. Substance gelatinous. *Siphons.* 8–10 pericentral sometimes bounded by a row of corticating cells at the base. *Colour.* Brownish-red. *Anatomy.* Articulations from 1–2 or seldom three times longer than their breadth in the upright parts of the plant, and about equal to their breadth in the prostrate portions near the attachment organ. *Attachment organ.* Numerous rhizoids formed from the pericentral siphons or the corticating cells when the latter are present, the rhizoids developing disc-like expansions at the tips when they encounter a firm substratum. *Reproductive organs.* Tetraspores intercalary in development, borne in swollen ramuli. Cystocarps ovate in form, with a conical elongation towards the ostiole.

According to Hauck (31. p. 240), the species is ecorticate, but in the lower parts of the main branches a row of corticating cells sometimes occurs, the individual cells of which alternate with the pericentral siphons. The ramuli are described by De Toni (22. p. 924) as having "apice non penicilliferis," but in a specimen obtained from Swanage, April 1919, there were clusters of filamentous hairs at the tips of the ramuli. The error is probably due to the previous examination of the plant having taken place at a different time of the year. When the plant grows on another alga, e. g. *Codium adhaerens* (Durlston Head, Swanage), attachment discs are not developed at the tips of the rhizoids; a holdfast is obtained by the latter ramifying among the cells of the host.

Habitat. On rocks, stones, and on other algæ such as *Codium adhaerens* between the tide-levels. Very rare.

British Records. Brighton, Swanage (Batten, 1919), Plymouth, Falmouth, and Newlyn West.

Distribution in Europe. Adriatic Sea.

3. *P. FRUTICULOSA* Sprengel, Syst. veg. vol. iv. 1825, p. 350.
Rytiphlæa fruticulosa Harv. Phyc. Brit. pl. 220. syn. 105.
Hutchinsia Wulfeni C. A. Ag. Sp. Alg. vol. ii. 1828, p. 95.
Grammita Wulfeni Bonnem. Hydroph. loc. 1822, p. 27.
P. Martensiana Kütz. Tab. Phyc. xiv. 1864, p. 10, tab. 29 (a-c).
P. pycnophlæa Kütz. l. c. p. 10, tab. 30 (e-g).
P. comatula Kütz. l. c. p. 10, tab. 31 (a-c).

References. Agardh (2) ii. p. 1028 ; De Toni (22) iv. p. 950.

Icones. Harvey, Phyc. Brit. l. c. Kützing, Tab. Phyc. l. c. Falkenberg, Die Rhodomet. 1901, pl. 21 (1-5). *Ersicrata*. Wyatt, Alg. Damnon. no. 132.

DESCRIPTION.—*Habit.* Occurring in tufts from 10–15 cms. in height. Branching roughly pseudo-dichotomous in the main branches, with wide angle of divergence causing characteristically angular appearance. Smaller branches bi-pinnate, the whole plant being clothed with short spine-like ramuli set at a wide angle. Perennial species, cartilaginous in nature. *Siphons.* 8–12 pericentral, surrounded by a wide band of corticating cells. *Colour.* Dark brownish-purple. *Anatomy.* Articulations almost completely obscured throughout the plant by the corticating cells. When visible they are about as long as broad, except in the small branches and ramuli where their length is less than their breadth. *Attachment organ.* Rhizoids developed from siphons and corticating cells at the base of the original axis. Later, branches arising near the base creep along the substratum and bear laterals alternately, those on the upper side forming ‘shoots,’ the lower ones being modified to form attachment organs. The modified branches bear rhizoids profusely, frequently strengthening the holdfast by twisting round a portion of the coralline host. *Reproductive organs.* Tetraspores borne in swollen and distorted ramuli. Cystocarps rare, sessile and ovate in form when present, crowded on the ramuli.

The attachment organ of this species is of especial interest, resembling that of *Pterosiphonia* rather than *Polysiphonia*. It is the only British member of the latter genus which has branches specially modified to form attachment organs.

Habitat. Occurring in tide-pools on the rocky bottom, and particularly in warm shallow pools on *Corallina officinalis* and other coralline algæ. Occurring also in the low littoral zone when the *Fucus serratus* vegetation is not too dense. Common on the shores of the South of England, Ireland, and the Channel Islands, rare in Scotland and northern England.

British Records. Isle of Wight, Swanage, Weymouth, Sidmouth, Torbay, Plymouth, Looe (Batten, 1921), Falmouth, Penzance, Mount’s Bay, Trevone, Hilbre Island, Isles of Man and Anglesea, Arran, Cumbræ, Ballantrae, Portincross, Portrush, Bantry Bay, Miltown Malbay, Roundstone Bay, and the Channel Islands.

Distribution in Europe. Atlantic and Mediterranean shores.

4. *P. NIGRESCENS* Grev. in Smith's Engl. Flora, v. 1833, p. 332.

Conferva nigrescens Dillw. Brit. Conf. 1809, pl. 155.

P. violascens Kütz. Spec. Alg. 1849, p. 813.

P. regularis Kütz. Tab. Phyc. xiii. 1863, p. 16, tab. 51 (a, b).

P. sentosa Kütz. Tab. Phyc. xiii. 1863, p. 16, tab. 51 (c, d).

P. lophura Kütz. Tab. Phyc. xiii. 1863, p. 17, tab. 52 (c, d).

References. Agardh (2) ii. p. 1057; De Toni (22) iv. p. 940; Falkenberg (24) p. 129; Hauck (31) p. 244.

Icones. Dillwyn, Brit. Conf. 1809, pl. 155. Harvey, Phyc. Brit. 1846-51, pl. 277. syn. 122. Kütz. Tab. Phyc. l. c. pls. 51, 52 (c, d), 56 (f-i). *Essiccata.* Wyatt, Alg. Damnon. no. 135.

DESCRIPTION.—*Habit.* A perennial, occurring in tufts as much as 5 cms. in diameter, and varying from a slender plant about 7 cms. in length to a coarse form attaining a length of 30 cms. and having the lower parts clad with the broken remains of old ramuli. Branching variable but typically alternate, the branches subdividing and ultimately bearing large numbers of closely pinnate ramuli, which are themselves again doubly-pinnate and bear dichotomous fibrillæ at their tips. During the winter the ramuli disappear, leaving the plant with a serrate appearance. The substance is rigid except in the ramuli, which are flaccid and adhere to paper. *Siphons.* 12-20 pericentral, round a central one with diameter equal to about one-third of the diameter of the filament. At the extreme base a row of small cells frequently bounds the pericentral siphons on the outside. *Colour.* Brownish-purple. *Anatomy.* Articulations about as long as broad in the older parts, but attaining a length of $1\frac{1}{2}$ times their breadth in the smaller branches. *Attachment organ.* At the base of the main axis a number of rhizoids occur, formed from the longitudinal elongation of pericentral siphons. Later, when cortication develops, external cells aid in the formation of the attachment organ, and procumbent branches send off rhizoids from their creeping portions. The discs at the apices of the rhizoids are well developed, affording additional resistance to the force of the waves by their mechanical interlocking, the part actually coming in contact with the substratum being comparable to the base of the attachment in complex forms like *P. elongata*. *Reproductive organs.* Tetraspores borne in the ramuli and uppermost branches, frequently intercalary in development. Antheridia formed in yellow clusters at the tips of the ramuli, usually among clusters of multicellular hairs. Cystocarps broadly egg-shaped and almost sessile.

This species often bears a strong outward resemblance to *Pterosiphonia thuyoides* Sch., although the branching is not so regular. It may be distinguished with a hand-lens by means of the attachment organ, the tiny branches specially modified for attachment which are present in *Pterosiphonia thuyoides* being absent in *P. nigrescens*.

P. atro-purpurea Moore in Harv. Man. ed. i. p. 89, appears to be a variety of *P. nigrescens* with a more slender habit and corymbose ramuli. A variety which was brighter and more purple in colour with greater delicacy of ramification was described by Carmichael (28. p. 115) as *P. violacea*. This no doubt accounts for the one-time confusion between two species which are so distinct anatomically. A form with 16 siphons and long articulations has been separated by Moore as *P. affinis* in Ord. Surv. Londonderry, App. p. 11, t. 7, and figured by Harvey (28) t. 303. The siphons are somewhat twisted, but the twisting is very slight and variable. The plant shows lax growth, and combines corymbose branching with unusually long articulations and about 16 siphons. *P. dichoccephala*, figured by Kützinger (37) xiii. pl. 53, appears to be the same plant as that which Harvey describes as *P. affinis* Moore.

Material dredged in Plymouth Sound showed the antheridia of *P. nigrescens* growing directly on short stalks on the ramuli and not on dichotomising fibrillæ. Under these circumstances the multicellular axes of the antheridia frequently protruded from their tips.

Habitat. Attached to larger algæ, and on rocks and stones between the tide-levels. Common.

British Records. Common almost everywhere on the shores of the British Isles. Var. *P. affinis* Moore (= var. *ε. affinis* J. Ag.) : Mouth of R. Deben, Ramsgate, Eastbourne, Torbay, Carnlough near Glenariff, Cushendall, and the Channel Islands. Rather rare.

Distribution in Europe. Atlantic shores.

5. *P. VARIEGATA* J. G. Ag. Alg. Medit. 1842, p. 129.

Grammita Bonnem. in Journ. Phys. xciv. (1822) p. 186.

G. denudata Crouan, in Desmaz. exs. no. 1208, 1842 (excl. syn.).

P. leptura Kütz. Tab. Phyc. xiii. 1863, p. 28, tab. 89 (f-i).

P. denudata (fide Hauck) Kütz. Tab. Phyc. xiii. 1863, p. 28, tab. 90.

References. Agardh (2) ii. p. 1030; De Toni (22) iv. p. 922; Falkenberg (24) p. 119 et seq.; Hauck (31) p. 236.

Icones. Harvey, Phyc. Brit. 1846-51, pl. 155. syn. 119. Kützinger, Tab. Phyc. l. c. Thuret et Bornet, Études Phyc. 1878, fig. 42. *Ersiccata*. Desmaz. exs. no. 1208, 1842 (excl. syn.).

DESCRIPTION.—Habit. An annual, caespitose, tufts attaining a length of 25 cms. Branching pseudo-dichotomous, widely divergent, main axis flexuose. *Siphons.* 6 pericentral, surrounded by a band of corticating cells in the lower parts of the plant. *Colour.* Purplish-brown, with frequently a greenish tint in the principal branches. *Anatomy.* Articulations shorter than their breadth near the base of the plant, twice as long as broad in the principal branches, gradually becoming shorter upwards. *Attachment organ.* Plants attached by a disc at the base of the main axis, subsequently strengthened by rhizoids formed from the siphons and corticating cells of

small branches, arising near the original attachment organ. A disc-like expansion develops by the mechanical interlocking of the expanded bases of the rhizoids. *Reproductive organs.* Tetraspores small, intercalary. Antheridia occurring in large numbers near the tips of the branches. Cystocarps occurring on the smaller branches and ramuli, broadly ovate at the base and shortly stalked.

A floating species found in September (Cotton) in the lake of Poole Park exhibited marked dichotomy in the lower branches, and the articulations consisted of six pericentral siphons and a central one. No cortication was present. The mud-loving estuarine habit of the plant confirms the decision that the plants found were floating forms of *P. variegata*.

Habitat. A mud-loving estuarine species occurring on rocks, stones, and on smaller algæ such as *Chorda filum* and on the leaves of *Zostera*. Very rare.

British Records. Brighton, Isle of Wight, Studland (Batten), Swanage (Batten), Weymouth, Plymouth, Torpoint, and St. Minver.

Distribution in Europe. Atlantic shores of France and Spain, Mediterranean and Adriatic Seas.

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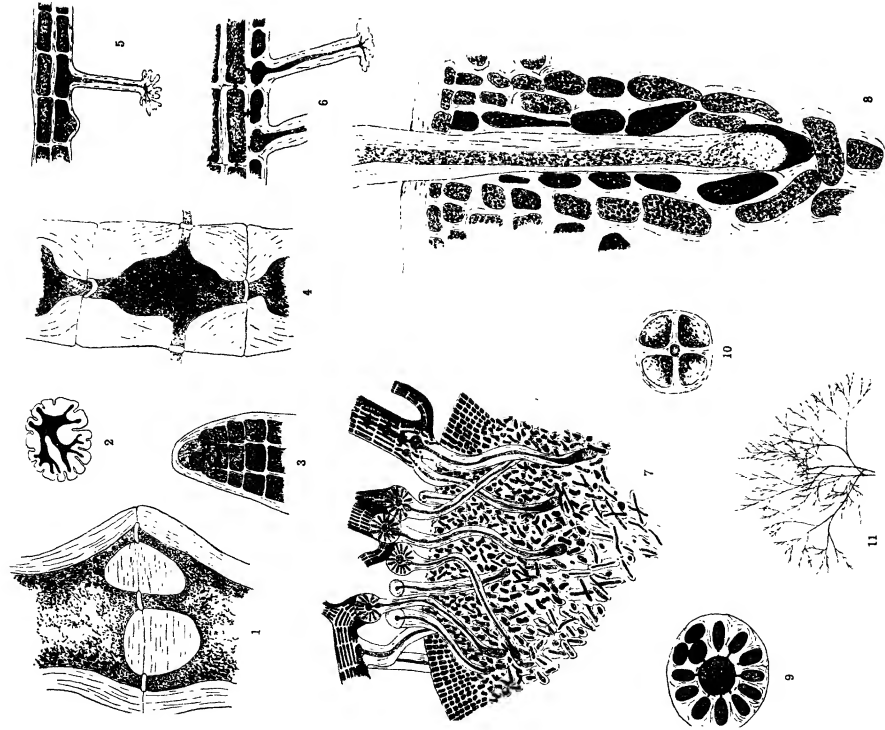
EXPLANATION OF THE PLATES.

PLATE 22.

- Fig. 1. Protoplasmic connections of the central siphon in *P. elongata*.
 2. Attachment disc of *P. fruticulosa*, seen from below.
 3. Tip of lateral branch of *P. urceolata*.
 4. Central siphon of *P. fastigiata*, showing protoplasmic connections and thickened walls.
 5. Development of rhizoids from the pericentral siphons of *P. macrocarpa*.
 6. Formation of rhizoids from the corticating cells in *P. nigrescens*.
 7. Transverse section of thallus of *Ascophyllum nodosum*, showing penetration by the rhizoids of *P. fastigiata* (constructed from a number of sections).
 8. T. S. of thallus of *Ascophyllum nodosum* at the point of penetration of *P. fastigiata*, showing decolorised cells which have been attacked. Cam. luc.
 9. T. S. of thallus of *P. fastigiata* in region bearing tetraspores.
 10. *P. insidiosa*. T. S. of thallus.
 11. " Habit drawing.
 12. *P. macrocarpa*. Portion of thallus showing attachment organs.
 13. " Habit drawing.
 14. " T. S. of thallus.
 15. *P. rhumensis*. Habit drawing.
 16. *P. spiralis*, spec. nov. Plan showing relative positions of twisted and untwisted portions.
 17. " Branch bearing tetraspores.
 18. " T. S. of thallus.
 19. " Portion of thallus showing spiral twisting of the siphons.
 20. " Habit drawing.
 21. " Portion of thallus showing attachment organ.
 22. " Branch bearing tetraspores.
 23. *P. urceolata*. Habit drawing.

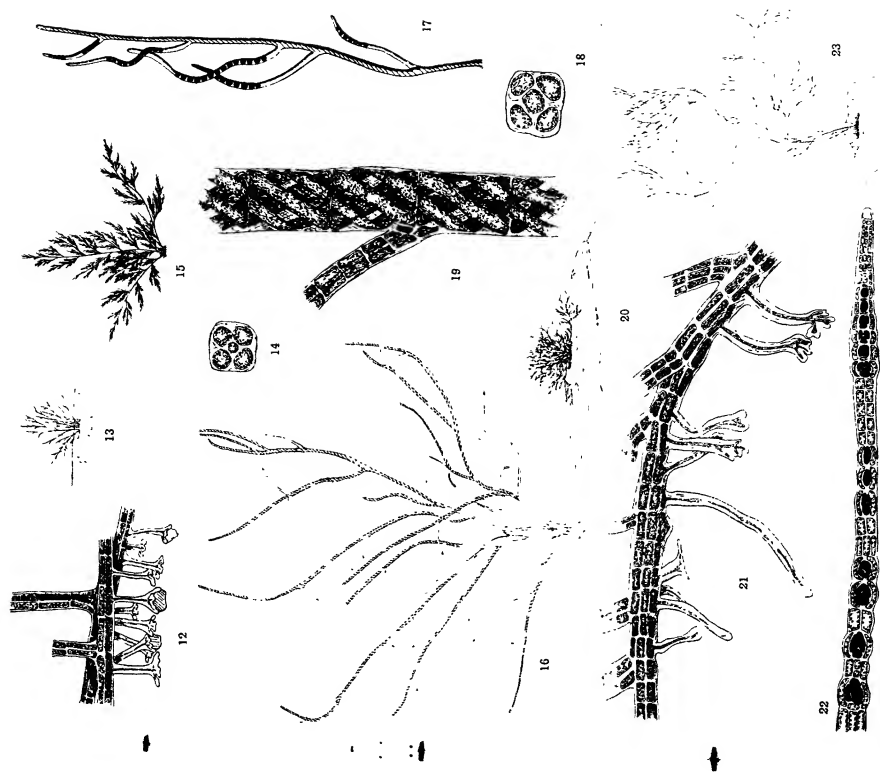
PLATE 23.

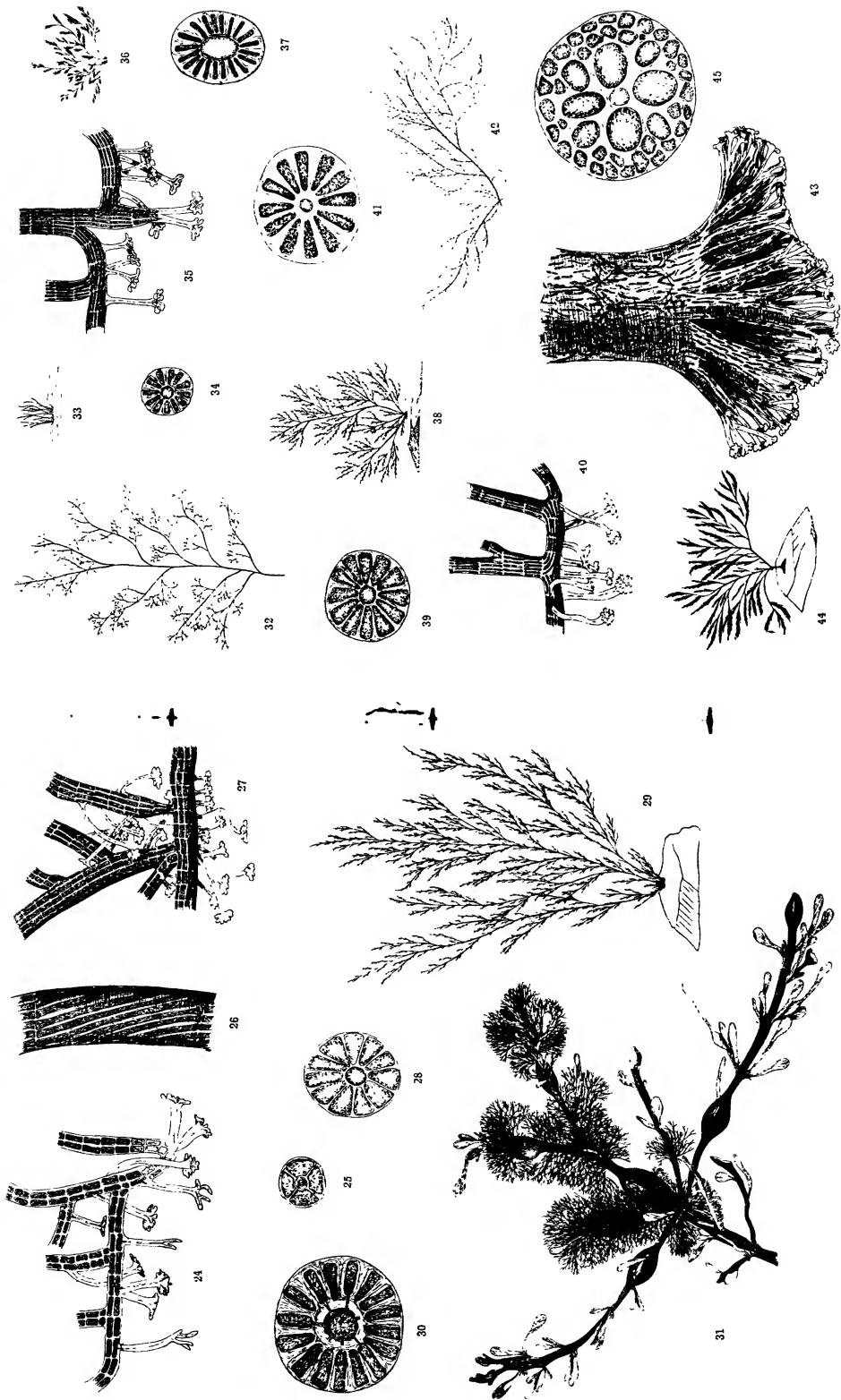
- Fig. 24. *P. urceolata*. Portion of thallus bearing attachment organs.
 25. " T. S. of thallus.
 26. *P. atro-rubescens*. Portion of thallus showing spiral twisting of the siphons.
 27. " Portion of thallus showing attachment organs.
 28. " T. S. of thallus.
 29. " Habit drawing.
 30. *P. fastigiata*. T. S. of thallus.
 31. " Habit drawing showing various stages in the development of the Polysiphonia on *Ascophyllum nodosum*.
 32. *P. furcellata*. Habit drawing.

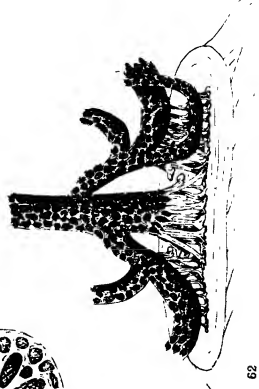
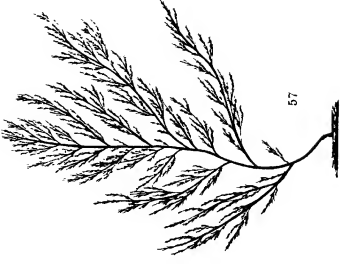
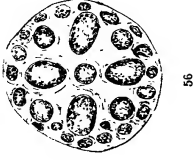
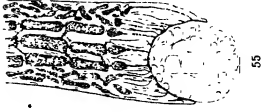
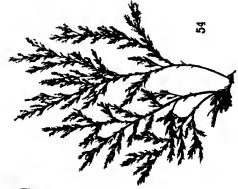
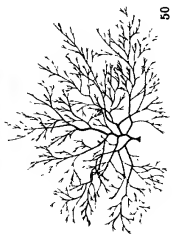
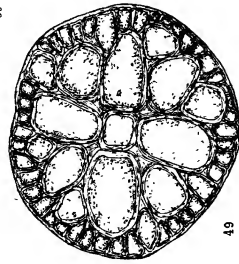
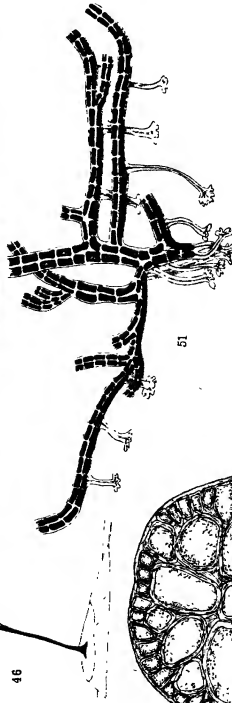
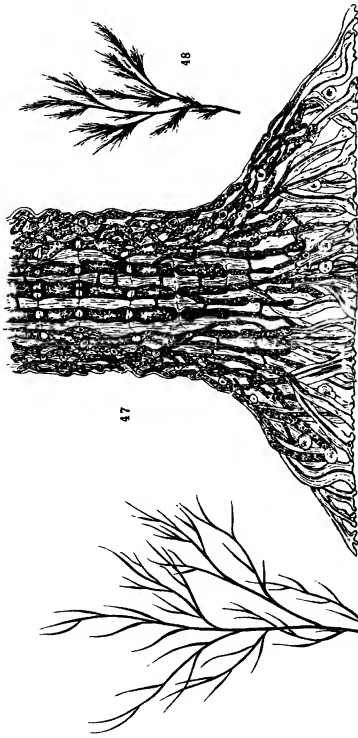


THE GENUS

POLYSIPHONIA.



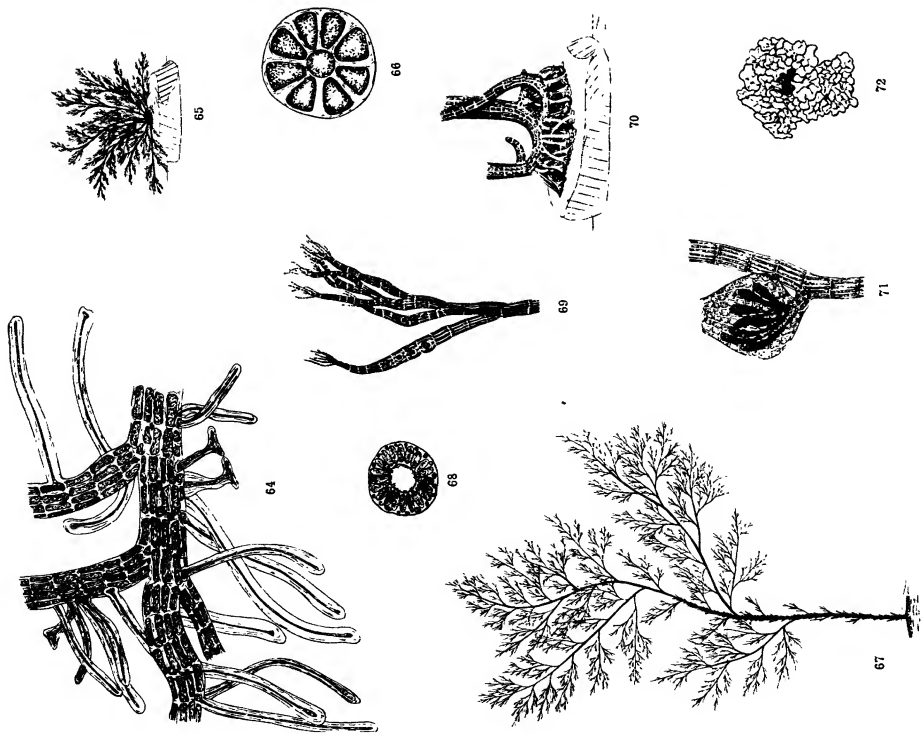




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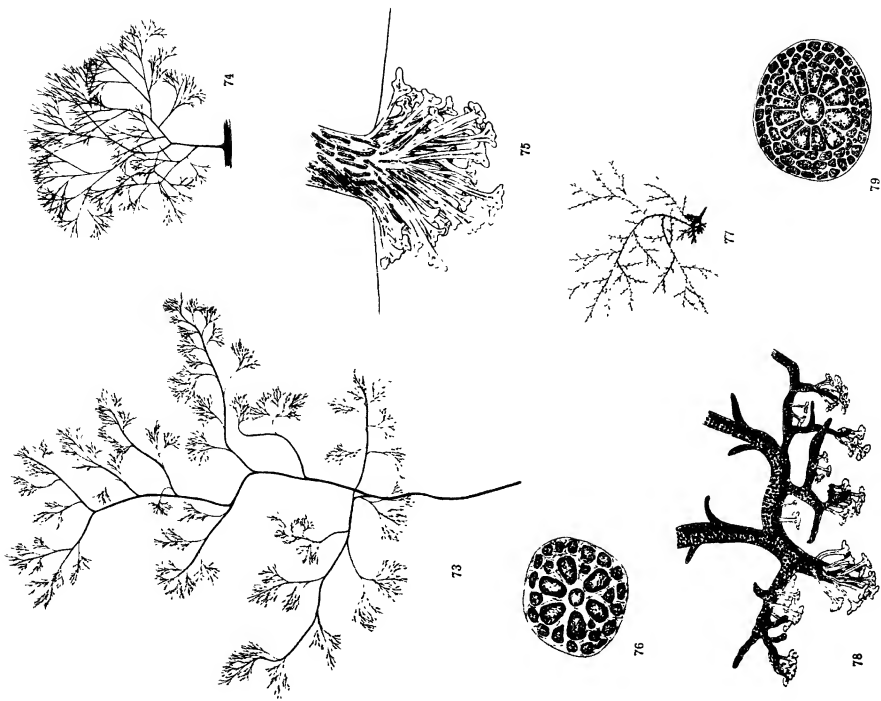
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THE GENUS

POLYSIPHONIA.



- Fig. 83. *P. obscura*. Habit drawing.
 34. " T. S. of thallus.
 35. " Portion of thallus bearing attachment organs.
 36. *P. opaca*. Habit drawing. (Herb. spec.)
 37. " T. S. of thallus.
 38. *P. simulans*. Habit drawing.
 39. " T. S. of thallus.
 40. " Portion of thallus showing attachment organs.
 41. *P. subulifera*. T. S. of thallus.
 42. " Habit drawing.
 43. *P. elongella*. Habit drawing.
 44. " Exterior view of attachment organ.
 45. " T. S. of thallus.

PLATE 24.

- Fig. 46. *P. elongata*. Habit drawing. (Winter state.)
 47. " Longitudinal section of thallus showing attachment organ.
 48. " Portion showing ramuli. (Summer state.)
 49. " T. S. of thallus.
 50. *P. Richardsoni*. (From Dr. Richardson's specimen, Nat. Hist. Mus.)
 51. *P. fibrata*. Portion of thallus showing attachment organs.
 52. " Habit drawing.
 53. " T. S. of thallus.
 54. *P. fibrillosa*. Habit drawing of plant on *Rytiphlea pinastroides*.
 55. " L. S. of attachment organ grasping thallus of *Rytiphlea pinastroides*.
 56. " T. S. of thallus.
 57. *P. violacea*. Habit drawing of plant on *Chorda filum*.
 58. " T. S. of thallus.
 59. " L. S. of thallus showing attachment organ
 60. *P. spinulosa*. (From herb. spec. Nat. Hist. Mus.)
 61. *P. Brodæi*. T. S. of thallus.
 62. " Portion showing attachment organ.
 63. " Habit drawing.

PLATE 25.

- Fig. 64. *P. foetidissima*. Attachment organs when growing on *Codium adhaerens*.
 65. " Habit drawing.
 66. " T. S. of thallus.
 67. *P. nigrescens*. Habit drawing.
 68. " T. S. of thallus.
 69. " Branch bearing tetraspores.
 70. " Portion showing attachment organ.
 71. " Cystocarp with carpospores.
 72. " Interlocking attachment discs seen from below.
 73. *P. nigrescens* var. *affinis*. Habit drawing.
 74. *P. variegata*. Habit drawing from herbarium specimen of Rev. W. S. Hore.
 75. " Portion showing attachment organ.
 76. " T. S. of thallus.
 77. *P. fruticulosa*. Habit drawing of plant on *Corallina officinalis*.
 78. " Portion showing attachment organs.
 79. " T. S. of thallus.

On the Occurrence and Distribution of *Festuca rubra*, Hack. in ~~Great~~ Britain. By W. O. HOWARTH, M.Sc., F.L.S., Lecturer in Botany in the University of Manchester.

(PLATES 26-30.)

[Read 14th December, 1922.]

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INTRODUCTION.

THESE notes on the occurrence and distribution of *Festuca rubra* in Britain are the outcome of research commenced in the neighbourhood of Cardiff in 1914. The necessity for distinguishing three forms of this grass found on different types of habitat led to a critical examination of Hackel's exhaustive Monograph on the European Festucas (1882). As a result it was determined to find out if, and how far, his system could be applied to all the British forms of this grass. A move to Manchester in 1919 gave access to the excellent collection of British and European plants in the Charles Bailey Herbarium, and since, the collections in the Herbaria at Kew and the British (Natural History) Museum have been compared. Great care has been taken in determining the plants on the numerous sheets: dissections, leaf-sections, glume measurements, etc. have been taken where possible in order that as great a degree of accuracy as can be obtained with herbarium material might be maintained. In addition, the living plant throughout has not been lost sight of, the author's collection having been supplemented by several kind friends who have sent samples for determination from various localities.

The descriptions here given are based on those of Hackel (*l.c.*), and Ascherson and Graebner (1900), but emended where it has been deemed necessary for our British plants from direct observation of the specimens themselves. Hackel's own descriptions admit of certain variations within a type, and for the purposes of this paper no single plant has been taken and described as a type specimen, but the sheets were first sorted out under their respective headings, and then the descriptions suited to the various plants under each heading.

Synonyms, where given, are additional to those of Hackel (*l.c.*).

The distribution of the various forms, obtained from the herbarium sheets and by the collection of living specimens, is shown by numbers corresponding

to Watson's vice-counties (1883). Types of habitat, where given, are from experience gained in collecting. It is hoped that the forms here brought together will be recognized by ecologists and their particular habitats recorded, so that their distribution can be worked out ecologically, at present impossible owing to lack of available data (the poverty of herbarium sheets in these details is well known). In the meantime it is hoped to test fully the distinctions made in order to confirm them or otherwise by experimental breeding. The author would be pleased to receive from any collectors material for determination, together with records of habitat and locality which can be incorporated in further work on this subject.

I. DESCRIPTION OF THE SPECIES.

The forms of *Festuca rubra* according to Hackel's system (1882) occurring in Britain are :—

Subsp. I. *heterophylla*.

„ IV. *eu-rubra*.

var. 1 (6). *genuina*.

subvar. α. *vulgaris* and its forms *pascua* and *nemoralis*.

β. *grandiflora* and its form *litoralis*.

γ. *glaucescens*.

δ. *juncea*.

ε. *barbata*.

ζ. *arenaria*.

var. 2 (7). *planifolia*.

var. 4 (9). *fallax*.

Subsp. V. *dumetorum*.

Reasons are given in the following pages for considering the group according to this arrangement and nomenclature, viz. —

Sp. I. *heterophylla* Lam.

„ II. *rubra* Linn. emend.

Subsp. 1. *fallax* Thuill.

2. *genuina* Hack.

var. α. *vulgaris* Gaud.

b. *grandiflora* Hack.

c. *tenuifolia* How.

d. *glaucescens* Hegets. & Heer.

e. *dumetorum* Linn.

f. *planifolia* Hack.

g. *juncea* Hack.

h. *arenaria* Osb.

Sp. III. *juncifolia* St. Am.

The various forms are accordingly described under these names.

F. RUBRA (Linn.) sens. ampliss. (Hack. 1882, p. 128).

(See also Aschers. & Graeb. 1900, p. 496.)

Plant with its branches either mostly intravaginal, or some or all extravaginal, the latter either directly ascending, or elongated and more or less creeping; turf thus either compact or loose. Sheaths of radical leaves entire; ligules glabrous; those of the radical leaves without auriculate margin, those of the cauline leaves unequally biauriculate or sometimes uniauriculate.

Key to Species.

- A. Ovary hispidulous, branches mostly intravaginal *heterophylla*.
- B. Ovary glabrous.
 - a. Intravaginal branches at least as many as extravaginal; leaves with blunt apex, 3-5-7-many-costate, each ridge with a corresponding isolated strand of sclerenchyma below lower epidermis *rubra*.
 - b. Branches all or mostly extravaginal; leaves with acute apex, 5-many-costate, sclerenchyma in a continuous layer below lower epidermis *juncifolia*.

Sp. I. **F. HETEROPHYLLA.** (See Hack. 1882, p. 130.) (Pl. 27.)

F. heterophylla Lam. 1778, p. 600.

- „ Koch, 1837, p. 813; 1844, p. 939; 1857, p. 705; 1907, p. 2773.
- „ Nym. 1878-82, p. 827; 1889, p. 338.
- „ Richt. 1890, p. 98.
- „ Aschers. & Graeb. 1900, p. 494.

Plant densely caespitose, branches mostly intravaginal, not creeping. Culm 4-9 dm. high; slender, weak, smooth. Radical leaves with entire trigonous sheath, and long, tightly complicate, entire, trigonous lamina, 0.4-0.6 mm. diameter, 3(-5) vascular bundles, each with corresponding subepidermal sclerenchymatous strand; 1-3(-5)-costate, motor cells absent (Pl. 26. fig. 1). Cauline leaves linear, 2-3 mm. broad, 7-11-nerved, (5-)7-costate, motor cells present. Ligules glabrous. Panicle 6-16 cm. long, lax, nodding, open at anthesis, basal branches 2-3, rhachi scabrous (fig. 1). Spikelets linear-oblong, 8-10 mm. long, 3-9-flowered, bright green. Sterile glumes subulate-lanceolate; fertile linear-lanceolate; 5-6.5 mm. long, somewhat rough on the back; awn half as long as the glume or longer, often somewhat wavy on the upper flowers. Ovary somewhat hairy above.

Var. *typica* (Hack.) has been found in England in a restricted area along the Thames valley represented by v.c.'s. 7, 12, 17, 22, 23. The earliest records are v.c.'s. 17 and 23 dated 1889. The grass is generally regarded as having been introduced, and its restriction to a small area as above suggests

that it may have spread from two centres, but Druce thinks it might be indigenous in the woods on the Bere Estate between Pangbourne and Bradfield (v.c. 22). See 6 *b.* pp. 322-3 ; 6 *c.* p. 405 ; 6 *g.* p. 288 ; and 6 *h.* p. 135.

Sp. II. *F. RUBRA* Linn. 1753, p. 74, emend. How. 1923 ; pp. 324 *et seq.* below.

F. eu-rubra Hack. 1882, p. 138.

„ Aschers. & Graeb. 1900, p. 497.

F. rubra Nym. Consp. p. 827 (incl. *F. fallax*).

„ Koch, 1907, p. 2774.

Forms a loose, or rarely, compact turf. Intravaginal and extravaginal branches about equal in number ; the latter creeping, or curved from the base, becoming erect. Sheaths of radical leaves entire, when dead scarcely and irregularly fibrous. Laminæ obtuse, keeled along the midrib on the under side, of radical leaves with 5-7 nerves and 3-5-7-costate ; a sub-epidermal separate strand of sclerenchyma usually corresponds to each vascular bundle on the under surface, and also at the margins, and less frequently, along the apex of each ridge of the upper surface. The entire group of forms shows marked similarity in the transverse section of the radical leaf (Pl. 26), which forms a very useful means of distinguishing members of this group from *heterophylla* or *juncifolia*, especially the latter. The culm laminæ are broader, flatter, with more numerous strands and bundles. Sterile glumes unequal, the upper extending to about the middle of the fertile one above it. Fertile glumes narrowly or broadly lanceolate, apex mucronate to aristate. Ovary glabrous.

Key to Subspecies.

1. Extravaginal branches all erect or nearly so *fallax*.
2. Stock decidedly creeping ; stolons bear brown scale-leaves *genuina*.

Subsp. 1. GENUINA.

F. eu-rubra, var. 1 (6) *genuina* Hack. 1882, p. 138.

„ „ „ Aschers. & Graeb. 1900, p. 497.

F. rubra Koch, 1857, p. 705.

„ Nym. Consp. p. 827 (excl. *F. fallax*).

„ Richt. Pl. Europ. p. 99 (excl. *planifolia*).

Loosely caespitose ; extravaginal branches at first more or less widely creeping, with brown scale-leaves, then becoming erect. Sheaths glabrous or puberulous. Radical laminæ folded, obtusely keeled, 5-7-nerved, -7-9 sclerenchymatous strands ; culm ones, flat or nearly so.

Key to Varieties.

1. Stolons shortly creeping.
 - a. Fertile glumes less than 6 mm. long, mucronate to aristate, glabrous or few short hairs near tip *vulgaris*.
 - b. Fertile glumes more than 6 mm. long, glabrous *grandiflora*.
 - c. Dark green foliage with "bloom" *tenuifolia*.

- d.* Foliage glaucescent; glumes with "bloom," glabrous or shortly hairy..... *glaucescens.*
e. Glumes covered with hairs *dumetorum.*
 2. Stolons extensively creeping.
 i. Spikelets glabrous.
 f. Leaves all alike, flat *planifolia.*
 g. Radical leaves narrow, keeled; culm ones flat *juncæa.*
 ii. Spikelets hairy *arenaria.*

(a) *VULGARIS.*

Subvar. *α. vulgaris* Hack. 1882, p. 139.

F. rubra, vulgaris Gaud. 1824, p. 285.

„ „ Aschers. & Graeb. 1900, p. 497.

„ type, Richt. Pl. Europ. p. 99.

„ subsp. *duriuscula* Syme, 1872, p. 145 (includes also var. *e*, and probably also *b*, *c*, *d*. and subsp. *fallax*).

Plant usually tall, with dark green foliage. Radical leaves setaceous, 0·5–0·6–1·0 mm. diam. (Pl. 26. fig. 4*a*). Panicle compact to loose; –18 cm. long. Spikelets 5–8–10 mm. long, bearing 3–7 flowers, lanceolate to broadly so, green or greyish-green, or feebly reddish-violet. Glumes smooth or may be rough about the tip and along the margins, averaging about 5 mm. long excluding awn, awn to 2 mm. long.

Distributed over the whole of Britain; actual records from v.c.'s. 1, 4, 5, 6, 8–12, 15–20, 23–27, 29, 31, 32, 36, 40–43, 53, 55, 57–62, 65, 69. Its caespitoseness varies according to the dryness of the situation and the nature of the soil.

Two forms, only probably habitat-forms, are:—

pascua Anderss. 1852, p. 20. Leaves shorter, panicle somewhat compact, spikelets mostly coloured greyish-violet. General habit low. Dry, exposed meadows etc.

nemoralis Anderss. l.c. p. 21. Leaves longer, panicle loose, spikelets green. General habit taller. Woods and sheltered situations.

(b) *GRANDIFLORA.*

Subvar. *β. grandiflora* Hack. 1882, p. 139.

F. rubra h. *macrantha* Richt. Pl. Europ. p. 99.

„ „ *megastachys* Aschers. & Graeb. 1900, p. 498.

Radical leaves larger (0·8–1·0 mm. or more diam.) (Pl. 26. fig. 4*b*); sheath somewhat hairy; panicle 10–18 cm. long, erect and open; spikelets 10–13 mm. long, 5–8 flowers; glumes smooth, green or greyish-green, more than 6·0 mm. long, awns up to 3·0 mm. long.

Recorded from v.c.'s. 4, 9, 11, 12, 14, 17, 19, 20, 21, 41, 54, 58, 59, 62, 69. A useful pasture grass on fairly well-drained soils, preferably, so far as one's experience goes, having a lime content.

Hackel has a form *litoralis*, named from specimens found on the salt-marsh at Wells, Norfolk, v.c. 28, by F. Long, with longer stolons and a low

habit, short compact panicles 2-4 cm. long, occurring only on the sea-coast in England (Pl. 26. fig. 4 b'). This appears to be merely a habitat-form. Dwarfing may be just the result of xerophytic conditions prevailing on the coasts; such conditions also usually result in greater caespitoseness (except in sand where it is the contrary), and a lighter green foliage approaching to glaucescence. Longer stolons, on the other hand, would bring it near to *juncea*, also a coastal plant. Forms which might be taken as *litoralis* occur also in v.c's. 14, 59, 60, 62, 69, but these cannot be given with any degree of certainty.

(c) *TENUIFOLIA*, mihi (1919, p. 267).

As *vulgaris* but radical leaves dark glaucous-green, 0.6-0.8 mm. diam. (Pl. 26. fig. 4 c); sheath slightly rough; panicle compact, open at anthesis, 6-9 cm. long; spikelets large, green, smooth, -12 mm. long, -8 flowers; glumes 6 mm. or more long, mucronate to aristate.

Appears to be confined to the Severn Estuary, where it forms a compact turf, much sought after, on the salt-marshes and older pebble ridges, and is periodically submerged by the highest tides. V.c's. 34, 35, 41.

(d) *GLAUDESCENS*.

F. glaucescens Heget. & Heer, 1840, p. 93.

F. rubra, genuina, subvar. *γ. glaucescens* Hack. 1882, p. 139.

„ var. *glaucescens* Nym. Consp. p. 827.

„ „ „ Richt. Pl. Europ. p. 99.

„ „ „ Aschers. & Graeb. 1900, p. 498.

Radical leaves glaucescent (sea-green), 0.5-0.8 mm. diam. (Pl. 26. fig. 4 d). Panicle 2.5-7.0 cm. long, compact, open at anthesis; spikelets 6.0-14.0 mm. long, 4-7 flowers; glumes usually of the *grandiflora* type, smooth or rough and always pruinous, glaucescent or rubro-violaceous.

The form originally described by Hegetschweiler and Heer has spikelets shortly hairy, hence this must be the true *glaucescens*, and the Monmouthshire forms (How. 1919, p. 268) agree. The smooth, glaucescent forms included here really belong to Hackel's *F. rubra, genuina, pruinosa* (6 a. p. 119), but the present author cannot see any very real difference between the two forms in herbarium material except that of the smoothness or roughness of the glumes above mentioned. According to Hackel it comes nearest to *juncea*, differing from this in its glaucous leaves, but in specimens examined there is no sign of the long stolons characteristic of *juncea*. It occurs in v.c's. 3, 6, 11. True *glaucescens* is found in v.c's. 1, 2, 3, 9, 11, 15, 34, 35, 58, 59, 60, 61, 62, 69, 70.

(e) *DUMETORUM*.

F. dumetorum Linn. 1762, p. 109.

F. duriuscula, dumetorum Host, 1797. p. 52.

„ „ Hudson, 1798, p. 44.

F. duriuscula, dumetorum Sm. 1798, t. 470 in text; 1800, p. 115.

„ „ Schrad. 1806, p. 328.

„ „ St. Am. 1821, p. 10.

„ „ Gaud. 1828, p. 109.

F. barbata Schrk. 1792, p. 46.

Tufted growth as *vulgaris*; radical leaves 0·7–1·1 mm. diam. (Pl. 26. fig. 4 *e*); panicle 11–14 cm. long; spikelets 8–11 mm. long, bearing 4–7 flowers; glumes shortly pubescent. Connected with the type through various intermediate stages. Some forms have large glumes as in *grandiflora*.

Distributed in v.c.'s. 10, 12, 18, 19, 20, 27, 32, 49, 55, 59, 62, 65, 66, 70. Found in the grasslands of sandy and gravelly soils, and on maritime sands, where it needs to be carefully distinguished from subvar. *arenaria*.

(*f*) *PLANIFOLIA*.

F. rubra, eu-rubra, var. 2 (7) *planifolia* Hack. 1882, p. 140.

F. planifolia Richt. Pl. Europ. p. 100.

Plant large. Stock widely creeping. Sheaths entire, glabrous or hairy. Laminæ all flat, 2–3 mm. broad (Pl. 26. fig. 4 *f*), many-nerved, separate subepidermal sclerenchymatous strands, motor cells present. Panicle large, loose, multispiculate; spikelets 9–10 mm. or more long, lanceolate, many-flowered, green or violaceous; glumes mostly broad-lanceolate, shortly awned.

In mode of growth very similar to *F. pratensis* (Huds. 1762, p. 37) and often confused with it, but the latter has split sheaths. Only two localities in Britain are recorded for this plant: Braunton, N. Devon, v.c. 4, and sandhills between Marske and Saltburn, N.E. Yorks, v.c. 62.

(*g*) *JUNCEA*.

F. rubra, eu-rubra, genuina, subvar. δ . *junceae* Hack. 1882, p. 139.

F. rubra, juncea Richt. Pl. Europ. p. 99.

„ *duriuscula* Aschers. & Graeb. 1900, p. 498.

Very widely creeping. Laminæ of radical leaves juncaceous (0·8–1·2 mm. diam., Pl. 26. fig. 4 *g*), rigid, glaucescent, subepidermal sclerenchymatous strands strongly developed; panicle mainly large, somewhat lax, 5–11 cm. long; spikelets large (9–10 mm. long), smooth, light greyish-green or with reddish hue; glumes in some forms 6·0 mm. or more long, shortly awned.

Undoubted specimens come from New Romney, Kent, v.c. 15, and Instow, N. Devon, v.c. 4. Others have been collected by the author from the Lancashire coast, v.c. 59 and 60. In the different herbaria are forms labelled "*arenaria*" and "*sabulicola*" which may belong to *junceae*, but it will be found that in patches of *arenaria* forms appear which have smooth glumes and yet are to be regarded as glabrous forms of *arenaria*, connected with this variety through various sub-glabrous stages. British collectors

have for some time recognized a form *sub-glabra* or *glabrescens* of *arenaria*, and there are undoubtedly glabrous forms connecting it with *junceae*. Hackel recognizes this.

(h) ARENARIA. (Pl. 28.)

F. rubra, eu-rubra, genuina, subvar. ζ . *arenaria* Hack. 1882, p. 140.

F. rubra, arenaria Koch, 1844, p. 939.

„ „ Syme, 1872, p. 147.

„ „ Richt. Pl. Europ. p. 99.

„ „ Aschers. & Graeb. 1900, p. 499.

F. rubra Sm. 1800, p. 116 in part; 1809, t. 2056; 1832, p. 61.

F. arenaria Osb. 1805, p. 4.

Extensively creeping. Leaves fairly rigid, 0.9 or more mm. diam. (Pl. 26. fig. 4 h). subepidermal sclerenchymatous strands usually strongly developed but distinct; panicle 7–13 cm. long; spikelets usually large, elliptico-lanceolate, 9–13 mm. long, bearing 4–8 flowers; sterile glumes unequal, fertile ones broader above the lower half (contrast *juncifolia*), surface densely hispid or villose.

No doubt well distributed around our coasts although actual records are from v.c's. 3, 4, 6, 10, 11, 19, 27, 28, 48, 54, 58, 59, 60, 62, 66, 67. It must not be confused with either var. *dumetorum*, or Sp. *juncifolia*.

Subsp. 2. FALLAX. (Pl. 29.)

F. fallax Thuill. 1824, p. 50.

„ Richt. Pl. Europ. p. 100.

F. rubra, eu-rubra, var. 4 (9) *fallax* Hack. 1882, p. 142.

F. rubra, fallax Nym. 1878, p. 127; 1889, p. 338.

„ „ Koch, 1907, p. 2774.

Densely caespitose; extravaginal branches (fewer than intravaginal ones) bend upwards at once and do not creep. For the rest as var. *genuina* and parallel to it. It occurs as ~~sub~~vars. *grandiflora* and *barbata* as in *genuina*. Apart from the root-stock it is impossible definitely to distinguish the two varieties, but certain aids to identification are found in the greater inequality of the sterile glumes: in *fallax* the first is less than two-thirds the second; the fertile glumes are also more slender, gently tapering to the awn, and the awns longer in proportion. On account of its habit it has been frequently confused with *F. ovina*, but the differences are well marked, as is set forth below. Its occurs commonly as a constituent of the chalk grassland (e. g. the Downs), and much that has been ascribed to *F. ovina* is really *F. rubra, fallax*. It also occurs on the limestone of S. Wales and Derbyshire. According to Schroeter (1908, p. 294) it extends to a height of 2760 m. in the Alps, and forms in places an almost pure turf. In Britain it has been collected from v.c's. 8, 12, 15, 16, 17, 22, 34, 38, 41, 55, 57.

~~Sub~~var. *barbata*, v.c's. 4, 22.

F. ovina.

1. Branches all intravaginal and directly ascending.
2. Leaves all alike, setaceous.
3. Radical sheath split almost to base.
4. Radical lamina in transverse section has a continuous or only slightly discontinuous stratum of subepidermal sclerenchyma.
5. Culm below panicle usually tetragonal, and rough.

F. rubra, fallax.

1. Some branches extravaginal, but more or less directly ascending.
2. Radical leaves setaceous, cauline ones flat or nearly so.
3. Radical sheath entire throughout its length.
4. Radical lamina in transverse section has separate small subepidermal strands of sclerenchyma, one below each vascular bundle (Pl. 26. fig. 3).
5. Culm below panicle usually terete and smooth.

Sp. III. *F. JUNCIFOLIA* St. Am. 1821, p. 40. (Pl. 30.)

F. rubra subsp. *dumetorum* Hack. 1882, p. 145 (non Linn. 1762).

F. dumetorum Nym. 1878, p. 827 : 1889, p. 338.

„ Richt. Pl. Europ. p. 101.

F. sabulicola Duf. 1825, p. 85.

F. rubra α, Sm. 1800, p. 116, Yarmouth specimen.

F. arenaria Bréb. 1859, p. 358.

„ Bor. 1857, p. 715.

Stock scarcely caespitose ; all or the majority of the branches extensively creeping. Culms tall (20–40 cm.), stout, rounded, smooth. Sheaths glabrous, irregularly fibrous on decaying. Laminae similar, complicate, juncaceous, subcylindrical (1.0 mm. or more diam.) (Pl. 26. fig. 2), rigid, glaucescent, internally puberulous, extending into a narrow, acute point, in transverse section 7–11-nerved ; a continuous zone of subepidermal sclerenchyma below in several layers, sometimes united with the bundle sheath of the midrib, rarely discontinuous, 5– or more costate, each ridge with separate sclerenchymatous strand below upper epidermis. Panicle small (4–10 cm. long) or large (–18 cm. long), contracted or loosely effuse. Spikelets large, 9–11 mm. long, shortly pedicellate (–1.0 mm. long), elliptical or elliptico-lanceolate, yellowish-green. Sterile glumes subulate-lanceolate, subequal, acute ; second 3-nerved, lateral ones running almost to apex, 2/3rds to 3/4ths length of fourth. Fertile glumes lanceolate or linear-lanceolate, broadest in the lower half, and from there gradually tapering to the tip, 6–7 mm. long, often villose, mucronate or shortly aristate.

A form growing in damper places on the coast at Skegness, Lincoln, v.c. 54, with broader and flatter leaves has been named by Hackel forma *planifolia*. The leaves retain the pungent apex. (See 6d. p. 38, and e. pp. 141–2, also f. p. 174.)

Many of the plants placed under “*dumetorum*,” or “*sabulicola*” in the different herbaria are really *rubra*, *arenaria*. The characters of the glumes, etc. often leave one undecided, but the unfailing test is to be found in the

transverse section of the radical leaf. True *juncifolia*, whilst of rare occurrence in this country, is probably of wider distribution than we have been led to believe. On the East Coast it has been collected from Yarmouth district, v.c. 27, Skegness, v.c. 54, Southwold, v.c. 25, and on the South Coast at Exmouth, v.c. 3 (Kew Herbarium. under "*F. duriuscula*, var. *marina*"), and at Poole, v.c. 9 ("*F. rubra* var. *sabulicola*"). This latter seems to be a narrower leaved form (0.6 mm. diam. and 5-costate); but the record is further interesting as Woods (1848. p. 261) says:—"Towards the harbour (Poole) the sandhills yielded me *Festuca rubra* of the form which has been called *sabulicola* by some continental botanists."

II. EXAMINATION OF THE GROUP.

It is clear that whilst Hackel's system may be an excellent analysis of a difficult and complex group, yet the application of his long strings of names is, to say the least, cumbersome. Both *heterophylla* (Lam.) and *juncifolia* (St. Am.) stand out distinctly from the rest. In fact it seems that *F. heterophylla* has no place in the *ovina-rubra* group, and must be placed apart as a distinct species, mainly on the characters of its ovary and its radical leaf. *F. juncifolia* (St. Am.) has similar claims. Placed side by side with *F. rubra*, or better with the form *arenaria* of *F. rubra*, the two are unmistakable. In both panicle and leaf characters they differ, the outstanding differences being:—

F. rubra, *arenaria*.

F. juncifolia.

- | | |
|--|---|
| 1. As many intravaginal as extravaginal branches. | 1. Branches mostly or all extravaginal. |
| 2. Laminae, blunt apex. | 2. Laminae, sharp point. |
| " keeled in transverse section. | " complicate (suborbicular). |
| " 5-7 nerves. | " 7-11 nerves. |
| " 3-5-7-costate. | " 5-pluri-costate. |
| " scler. distinct. | " scler. continuous. |
| 3. Sterile glumes unequal. | 3. Sterile glumes subequal. |
| 4. Fertile glumes broader about or above the middle, aristate. | 4. Fertile glumes broader in the lower half, mucronate or shortly aristate. |

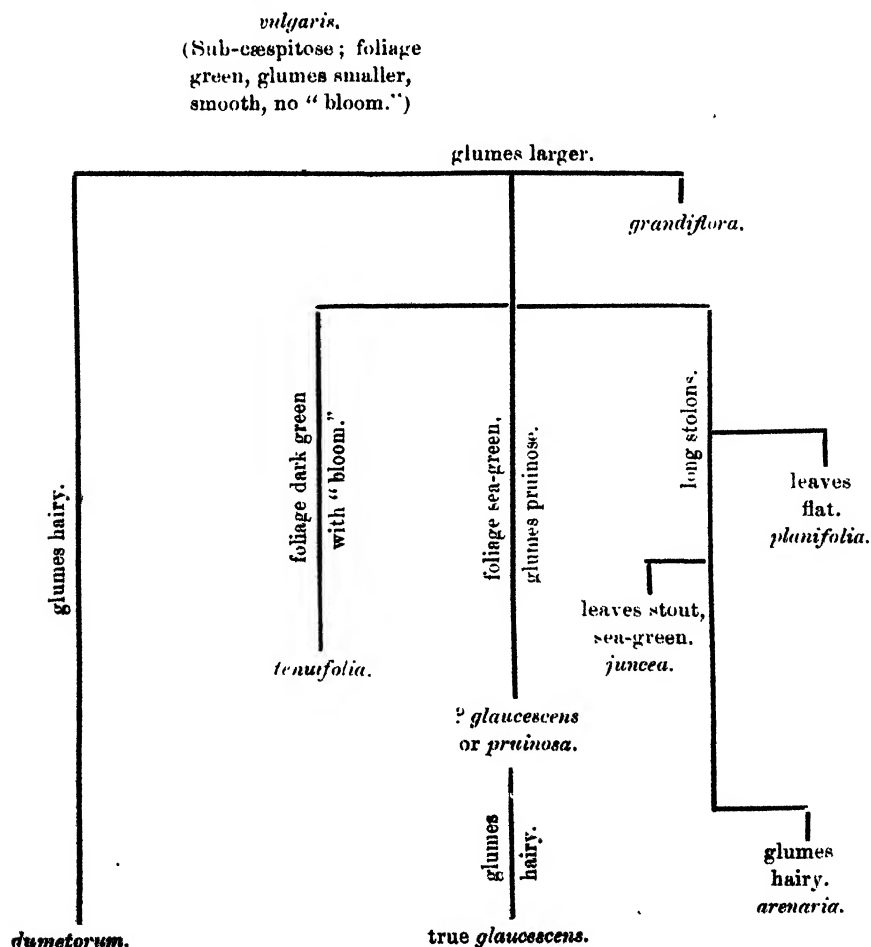
We have, then, as distinct species, *F. heterophylla* (Lam.) and *F. juncifolia* (St. Am.), and this leaves us with *F. eu-rubra*, which is here correspondingly treated specifically as *F. rubra*. Under *F. rubra*, *genuina* and *fallax* fall into two natural and parallel groups, as we have seen, distinct in vegetative habit. They can rightly be regarded therefore as two subspecies of *F. rubra*. Occasional intermediate forms are met with,—for instance, Hackel has determined one as "*genuina vulgaris* ad var. *fallax* vergens,"—but the division can be maintained by regarding forms which have anything in the nature of stolons, however few, as belonging to *genuina*, and reserving the strictly caespitose forms as *fallax*. Subsp. *fallax* is more restricted in its distribution than is subsp. *genuina*, and in this country at any rate seems to

have a very definite liking for calcareous soils. In the Alps, where it covers wide stretches according to Schroeter (1908, p. 294), it is found on all soils.

Hackel's var. *planifolia* is very rare. It seems to fit in more readily under *genuina* since it materially differs from the forms of the latter only in its flat radical leaves.

All Hackel's forms of *genuina* occur in this country. There is much to be said in favour of considering these forms as distinct and regarding them as true varieties. So far as experiment has gone they breed true and remain so under cultivation. They obey very definite laws as to their distribution, and remain distinct even though occurring together in the same habitat, or in the same locality but on different soils. Further experiment is being done to test this for all the forms, but it is certainly true regarding some of them. (Howarth, 1920.)

To show how in a general way these forms hang together the following table has been arranged :—



Var. *vulgaris* has the widest distribution, both inland and on the coasts. Vars. *dumetorum* and *grandiflora* have also inland and coastal stations. In *dumetorum* there is a tendency to large glumes, but on the whole it may be taken as a small-glumed form, directly linked with *vulgaris* through intermediate forms in different stages of hairiness. The *grandiflora* character enters very largely into all the other forms. By far the majority of the specimens examined under these forms have large glumes. From this group a line splits off having long stolons, and includes vars. *planifolia*, *juncea*, and *arenaria*; the sub-cæspitose line containing vars. *tenuifolia* and *glaucescens* (including *pruinosa*).

Subsp. *fallax* occurs in Europe as forms *grandiflora* and *barbata* according to Hackel, and also has habitat-forms, e. g. *pascua* and *nemoralis*.

III. "F. RUBRA" and "F. DURIUSCULA."

The Latin name *F. rubra* is first used by Linnæus in 1753 (p. 74), but he refers here to a description of Rüd-Swingel in 1745 (no. 92), which, however, he slightly emends in reproducing:—

Festuca paniculata secunda scabra, spiculis septi- ("sex-" 1753) *floris aristatis, flosculo ultimo mutico, culmi lævi* ("lævi" omitted 1753, "semitereti" added).

Gramen alpinum pratense, panicula duriora laxa spadicea. locustis majoribus (Scheuchl. gram. 287).

Hab. ubique in Suecia, præsertim in Uplandia. (Replaced in 1753 by "Hab. in Europæ sterilis siccis.")

Obs. Culmus lævis est, sed intra paniculam scaber, colore est culmus viridi, sed maturus rubet (omitted in 1753).

Magnitudine, colore maturatis rubro, culmo tereti sed altero latere planiusculo, distinguiter a F. ovina.

In his herbarium he wrote up a sheet bearing two panicles of *F. rubra*, *genuina*, *arenaria* from Lapland as *F. rubra*, and referred to his 'Flora Lapponica' (1737, no. 52), but this is the only such reference, and we cannot regard the herbarium specimen as the type, for var. *arenaria* is confined to maritime sands whereas Linnæus's *F. rubra* is "everywhere in Sweden," and "in Europe in dry, waste ground." The various descriptions imply that *F. rubra* L. includes all the obviously creeping forms, such as vars. *vulgaris*, *grandiflora*, *juncea*, and *arenaria* of the preceding pages, and is therefore an aggregate. Smith apparently regarded it in this light. In 1800 (p. 116) he describes *F. rubra*: "*Panicula secunda, flosculis teretiusculis aristatis, foliis supra pubescentibus, radix repente*" and "*Radix repens, flagellis longissime (in maritimus) per arenam mobilem extensis flosculi sæpius apice margineque tantum pubescentes, dorso glaberrimo*

at interdum in maritimus undique villosi." Then he refers to several specimens some of which are in his herbarium, the property of the Linnean Society. These the present author determines as follows :—

- i. "At Yarmouth, Mr. Woodward," is *F. juncifolia* St. Am., though not so robust as the type. Another plant on the same sheet is *F. rubra, genuina, glaucescens*.
- ii. "Scarborough, Mr. Teesdale," is *F. rubra, genuina, arenaria*.
- iii. "Dumfriesshire, Mr. J. Burgess," and
- iv. "Near Kirkby Lonsdale, Westmorland, 1783," are *F. rubra, genuina, vulgaris*.

Later, however, Smith (1809, t. 2056) under *Festuca rubra* figures var. *arenaria*, no doubt influenced by Linnæus's herbarium sheet, but in his description he refers to alpine specimens having a less spreading root. In 1832 (p. 61) he definitely states: "Root extensively creeping. Inhabits loose barren sands of the sea coast." He therefore ultimately limits *F. rubra* to var. *arenaria*. At the same time he relegates the more cæspitose forms with a tendency to a creeping root to *F. duriuscula*. Linnæus never refers to the glumes of *F. rubra* being glabrous or hairy, although he makes these characters a point of difference between his *F. duriuscula* and *F. dumetorum*. Haller (1742, p. 210, no. 9, and 1768, p. 215, no. 1440) describes the glumes as sub-hirsute and lightly sub-hirsute. Leers (1789, p. 32, no. 76) describes the spikelets as pubescent.

A study of the descriptions of *F. duriuscula* will help us further to elucidate the problem. Linnæus's first description of this grass (1753, p. 74) is that of Royen slightly emended. Thus Royen (1740, p. 68, no. 7) has :—
 "Festuca foliis setaceis, radicalibus minoribus, panicula inferne ramosa nutante, spicis adscendentibus hispidis. Ray hist. 1286, syn. 413. Bauh. hist. 2. p. 463."

Linnæus alters the order, quotes the descriptions of Ray and Bauhin and adds a reference to Scheuchzer :—

"Festuca panicula nutante inferne ramosa, spicis adscendentibus hispidis, foliis setaceis. Roy. lugdb. 68.

Gramen pratense, panicula duriore laxa unam partem spectante. Ray. hist. 1286, Scheuch. gram. 285.

Gramen tenue duriusculum et pene junceum. Bauh. hist. 2. p. 463.

Habitat in Europæ pratis siccis."

On critically examining the above references we find that the plant described by Ray (1285, not 1286) is a form of *F. rubra*, whilst the descriptions of Scheuchzer and Bauhin, and the figure of the latter, suggest a form of *F. ovina*.

In 1763 (p. 108) Linnæus adds his own description :—"panicula secunda

oblonga, spiculis sexfloris oblongis lævibus, foliis setaceis," and gives an additional reference to Ray (1724, p. 413, t. xix. fig. 1). On p. 109 he describes for the first time *F. dumetorum* :—"panicula spiciforme pubescente, foliis filiformibus. Hab. in Hispania.

Culmi pedales v. sesquipedales, filiformes, teretes geniculis duobus tumidis. Folia Radicalia pedalia, teretia, vix ancipitia; Caulina breviora, canaliculata. Panicula parva, quasi spicata. Spiculæ 10 s. 12, oblongæ, pubescentes, canescentes: inferiores geminæ, pedicellatæ; superiores sessiles, solitariae. Glumæ terminatæ arista minuta. Figura Moris. hist. 3, f. 8, t. 2. f. ult. hanc refert. Bulbi sæpe prognascuntur intra vaginæ culmi. Affinis valde *F. duriusculæ*."

In 1767 (p. 96) under *F. duriuscula* Linnæus says :—"Convenit cum *F. dumetorum*. Foliis radicalibus filiformibus canaliculatis; caulinis planis gramineis; Differt vero Glumis lævibus."

In his herbarium there is a sheet (no. 10) on which is pencilled in Smith's handwriting "*duriuscula*, Sp. Pl. ed. 1"; and a label written "gramen loliaceum, vol. 1, pag. 336, no. 5" is by Allioni and refers to Seguiet (1745). Smith must have had some authority for thus naming the plants because he calls them Linnæus's own specimens (1798, t. 470 in text). There are six plants on the sheet. One is *F. capillata* Lam. (*F. tenuifolia* Sibth.). Of the five remaining only panicles are mounted, so that it is exceedingly difficult to determine them with certainty. Four strongly suggest *F. rubra*, *fallax*, *forma barbata*, since they have hairy spikelets, the sterile glumes are very unequal and the fertile ones slender, tapering to a long awn; but they may belong to *genuina*, *barbata*. The fifth panicle certainly suggests a form of *F. rubra*, *genuina* on account of its large size and large, glabrous, almost mucronate glumes. In emending his description of *F. duriuscula* (1763) it is possible that Linnæus recognized this difference between glabrous and hairy glumes, retaining the one glabrous form as emended *duriuscula* and regarding the four hairy forms as *F. dumetorum*. This seems to be confirmed by his two sheets of *F. dumetorum*. The one (Sheet no. 7) was first written up by Linnæus, *Festuca duriuscula*, but he later put his pen through *duriuscula* and wrote *dumetorum*. On the back of this sheet he wrote, "Valde affinis *F. duriuscula* sed spiculæ pubescentes." This is precisely what he emphasizes in 1763 and 1767. He evidently wrote his first description of *F. dumetorum* on the basis of this plant which he raised from seed in the Uppsala garden, and we may rightly regard it as the type. It is interesting to note, however, that this plant is not *F. dumetorum* in Hackel's sense, but *F. rubra*, *genuina*, *barbata*. So is the plant on the other sheet (no. 8), formerly mistakenly named "*nodosa*" on account of nodal swellings on the culm due to insect infection, later renamed by Linnæus *F. dumetorum*. Panicle differences between forms of *F. rubra*, *fallax* and *F. rubra*, *genuina* are very slight and not easily noticed, so that it is conceivable that Linnæus

would include *fallax*, *barbata* and *genuina*, *barbata* under his *F. dumetorum*, and glabrous forms of *genuina* and *fallax* under his *F. duriuscula*. The latter plant is therefore the more caespitose, and our conclusion that *F. rubra* is the more obviously stoloniferous is confirmed.

This explanation is the only one which gives uniformity to Linnæus's descriptions and herbarium specimens. If we follow Hackel we must neglect the evidence of the herbarium sheets and attempt to form a comparison between Hackel's scarcely tufted, extensively creeping *F. dumetorum* and his *F. duriuscula* included under *F. ovina*, which has no stolons whatever. The acceptance of Hackel's *F. dumetorum* as that of Linnæus may account for the fact that some authors have regarded *F. duriuscula* as a more extensively creeping form than *F. rubra*.

Smith (1798, t. 470) was right when he wrote:—"The leaves of both (i. e. *duriuscula* and *dumetorum*) minutely ciliated or downy; and sometimes the outer husk, as well as the calyx, is all over clothed with soft pubescence, which makes the character of Linnæus's *F. dumetorum*; nor can we in his own specimens find any other mark than this, which is a variable one. Indeed, his specimens of *F. duriuscula* are some of them downy." But in describing *F. rubra* in 1809 (t. 2056) he observes that his forms of this grass are not really distinct from his *F. duriuscula*. The latter has a "tendency to a creeping root" and is connected through intermediate stages with *F. rubra* where "that part is indeed prodigiously elongated." Thus also Hooker (1821, p. 38) includes *F. rubra* as a variety of *F. duriuscula*, distinguished by its creeping root, and Syme (1872, p. 145) divides the species *F. rubra* under subsp. I. *F. duriuscula* "Linn." Sm., caespitose (i. e. *fallax*) or sub-caespitose (i. e. *genuina*, *vulgaris*, etc.), rootstock shortly creeping, stolons very short; and subsp. II. *F. arenaria* Osbeck, not at all caespitose, rootstock very extensively creeping, stolons long, etc.

There is also much support among early European authors for our view. Leers's (1789, p. 32) description of *F. duriuscula* and his figure (2. t. viii.) apply to a form of *F. rubra*. Host's (1802, pp. 59-60) description and figure (t. 83) agree with *F. rubra*, *fallax*. De Candolle (1805, pp. 50-51) says of *F. duriuscula* that it "rarely occurs in such compact tufts as *F. ovina*," and his *F. cinerea* var. *a* (*F. dumetorum*) is "like *F. duriuscula* except for its hairy glumes," while *F. cinerea* var. *b* (*F. arenaria*) is "taller with larger spikelets." Schrader (1806, p. 328) refers his *F. duriuscula* to Host, Smith, and Leers above, and to *F. heterophylla* Haenke (*F. rubra*, *fallax* var. *alpestris*). His var. *a* has glabrous spikelets, and var. *b* with pubescent spikelets he refers to *F. dumetorum* L. Gaudin's (1811, p. 251) *F. duriuscula* is *F. rubra*, *fallax*, as also is that of Fries (1842, p. 6). Gaudin's (1828, p. 686) *F. dumetorum* and that of Schur (1866, p. 793) is *F. dumetorum* L.

It appears as though Pollich (1776, p. 101) gave the lead to those

European authors who assign the name *F. duriuscula* to a form of *F. ovina* :— “folia radicalia et caulina omnia setacea sunt, compressa, rigidiuscula ac dura, mucronata, angustissima etc.” In this he may have been influenced by Linnæus’s reference (1753, p. 74) to Scheuchzer and Bauhin. Mertens and Koch agree, and argue that their *F. duriuscula* must be that of Linnæus’s *Species Plantarum* (not *Systema Naturæ*) because he calls the leaves of his *F. duriuscula* setaceous and gives the habitat as dry meadows. But if we compare Linnæus’s descriptions in 1763 and 1767 we find that in both he uses the words “foliis setaceis.” They say also that no other plant grows in dry meadows than their *F. duriuscula*, but forms of *F. rubra*, *genuina* and *fallax* are very common, the former upon dry, sandy or gravelly meadows and heaths, the latter on chalk and limestone grasslands in Britain, and apparently on all soils in Europe. They recognize that in 1767 Linnæus probably had *F. heterophylla* Haenke before him ; why not in 1763 ? They suggest that the *F. duriuscula* of 1763 is not that of 1767. The reason for this is probably because in 1767 Linnæus says of *F. duriuscula* that it resembles *F. dumetorum* in its filiform, channelled radical leaves and its flat, grass-like cauline leaves, but differs in having smooth glumes ; whilst in 1763 he describes the radical leaves of *F. dumetorum* as rounded, scarcely two-sided. We must bear in mind, however, that in the latter case Linnæus was probably describing a fresh specimen from his garden, in which case the keeled nature of the leaf is not nearly so prominent as in dried herbarium specimens.

Hackel (1882, pp. 89 and 216) follows Mertens and Koch above in making *F. duriuscula* L. (1753 not 1767) a form of *F. ovina*, but so far as the present author can judge, there is no authority for this. He is convinced that *F. duriuscula* L. (1763, p. 108) includes glabrous forms of *F. rubra*, *fallax* and of the more cæspitose forms of *F. rubra*, *genuina* ; that *F. dumetorum* L. (1763, p. 109, and 1767, p. 96) is equivalent to *F. barbata* Schrk. (1792, p. 46) and possibly also form *barbata* of *F. rubra*, *fallax* ; and that *F. rubra* L. (1753, p. 74) includes the more obviously stoloniferous forms of *F. rubra*, *genuina*. Thus *fallax* merges into *duriuscula*, and the latter into *rubra*, so that it becomes necessary to adopt the plan and revised nomenclature outlined in Section I. of this paper.

The description of *F. juncifolia* St. Am. (1821, p. 40) is :—

“Panicule unilatérale, peu ample, velue ; feuilles filiforme, ferme ; languette courte, déchirée en forme de cils.

Descr. Racine rampante. Chaulme haut d’environ deux pieds, muni de deux ou trois articulations un peu renflées. Feuilles roulées, cylindriques, très longues, striés, de la grosseur d’une ficelle, les radicales longues d’un pied et au-delà, les caulinaires de 2 à 4 pouces. Languette à peine longue d’une demi ligne, déchirée en forme de cils, et non auriculée. Panicule peu ample, un peu en épi, devenant blanchâtre en vieillissant, ramifications

inférieures geminées, quelquefois solitaires. Épillets velus, oblongs, aplatis, longs d'un demi pouce, composés de six fleurons longs de quatre lignes, surmontés d'une arête très courte."

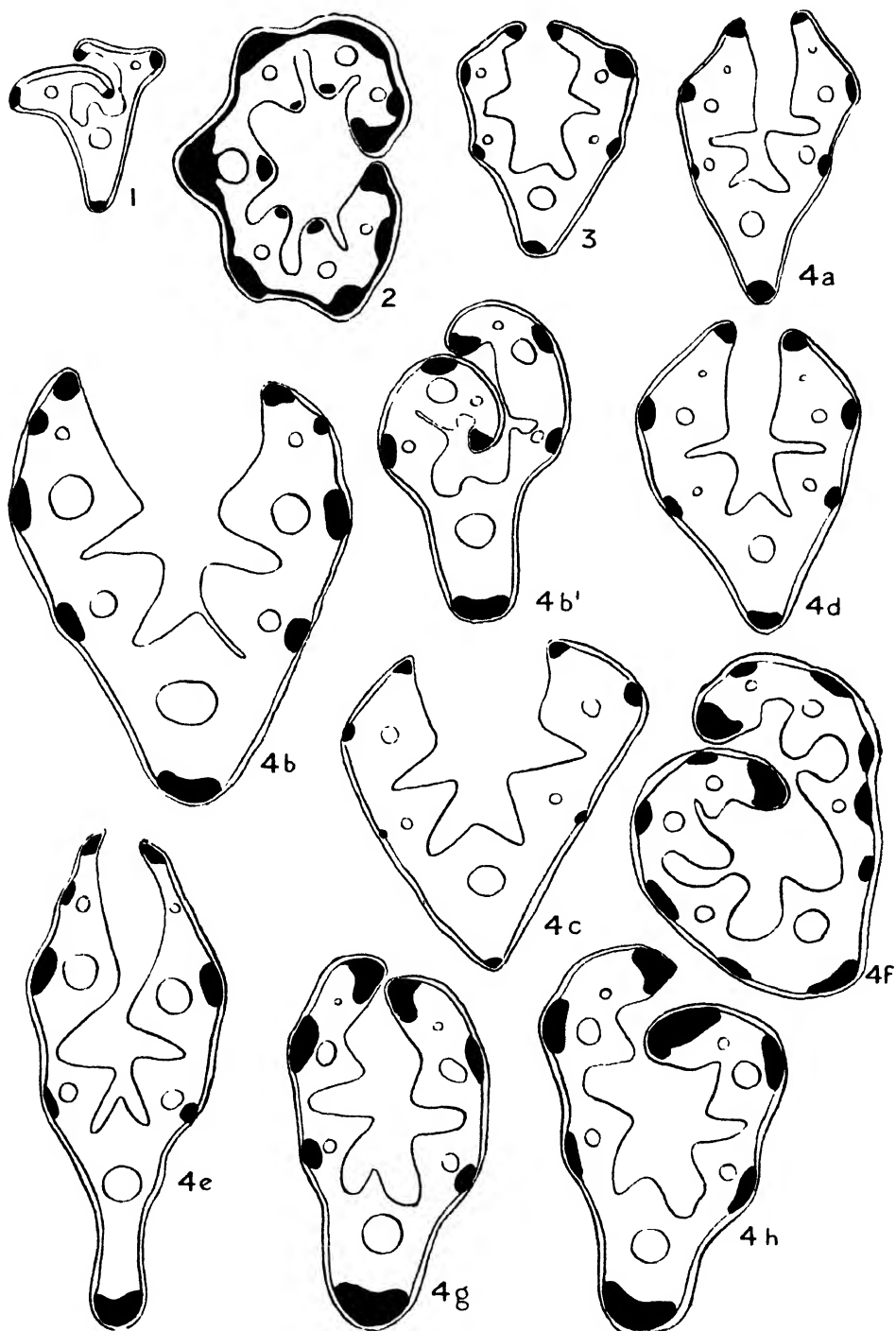
There has been some difficulty in placing *F. oraria* Dumort. Dumortier describes it under *F. rubra* (1823, p. 105), but he later (1868, p. 366) discusses this grass in relation to certain others. He denies that it is equivalent to *F. arenaria* Osb., and to *F. juncifolia* St. Am., but not to *F. sabulicola* Duf., for which he claims priority. The two last-named plants, however, appear to be identical, and were considered so by Hackel. Through the kindness of Dr. A. B. Rendle of the British Museum (Natural History) the type-specimen has been obtained from Brussels and examined by the author, who is satisfied that it is not *F. juncifolia* St. Am. (nor *F. sabulicola* Duf., nor *F. dumetorum* Hack.). On the whole it must be regarded as a large-glumed form of *F. arenaria* Osb., in spite of Dumortier's protestations to the contrary, since it agrees more closely with this than with any other of the vars. of *F. rubra*. It is a stoloniferous plant with foliage of the *F. rubra* type and culm about 80 cm. high. Its panicle is 17 cm. long, effuse; spikelets 13 mm., 4-7 fls., pedicels 1.5-3.0 mm. long, sterile glumes unequal, fertile ones -7.5 mm. long, villose, aristate. The size of *F. rubra*, *arenaria* varies considerably. Thus whilst in our British plants the glumes average 6.5 mm. in length, those of Linnæus' specimen gathered in Lapland are only 5.0 mm. long, and similar reduction in size is seen in plants from Spitzbergen and Novaya Zemlya.

The author expresses his indebtedness to Mr. A. J. Wilmott for criticism and valuable suggestions in revising the MSS., also his thanks to those who have either supplied fresh material, or dried plants from their herbaria: Prof. R. S. Adamson, Dr. G. C. Druce, W. P. Hiern, F.R.S., and C. E. Salmon.

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SECTIONS OF LEAVES OF FESTUCA.



W. O. H. phot.

Grout phot. s.

FESTUCA HETEROPHYLLA.



W. O. H. phot.

Grout phot. S.

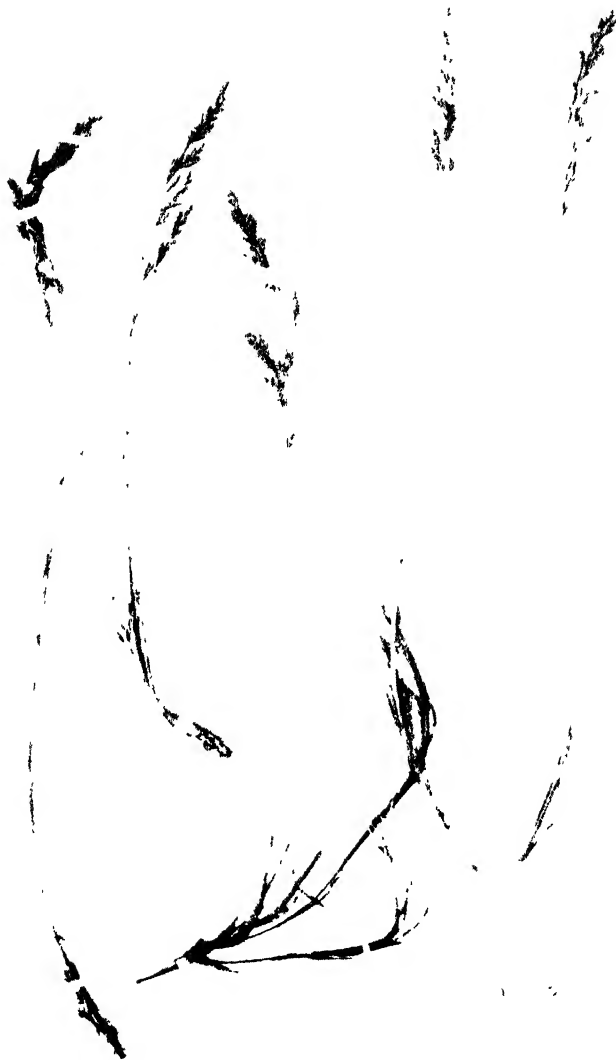
FESTUCA RUBRA subsp. **GENUINA** var. **ARENARIA**.



W. O. H. phot.

Grant, photo's

FESTUCA RUBRA subsp. **FALLAX.**



W. O. H. phot.

Grout phot. sc.

FESTUCA JUNCIFOLIA.

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EXPLANATION OF THE PLATES.

PLATE 26.

(Sections of Leaves.)

Fig. 1. *Festuca heterophylla*.

- | | | |
|-------|-----|---|
| 2. | " | <i>juncifolia</i> . |
| 3. | " | <i>rubra</i> , subsp. <i>var. fallax</i> . |
| 4. | " | var. <i>genuina</i> . |
| 4 a. | a. | subvar. <i>vulgaris</i> . |
| 4 b. | b. | —— <i>grandiflora</i> . |
| 4 b'. | b'. | —— ——— <i>forma litoralis</i> . |
| 4 c. | c. | —— <i>tenuifolia</i> . |
| 4 d. | d. | —— <i>glaucescens</i> . |
| 4 e. | e. | —— <i>dumetorum</i> . |
| 4 f. | f. | —— <i>planifolia</i> . |
| 4 g. | g. | —— <i>junceae</i> . |
| 4 h. | h. | —— <i>arenaria</i> . |

The above sections are enlarged about 60 diameters.

PLATE 27.

Festuca heterophylla, illustrating general habit. From a specimen in the Charles Bailey Herbarium, Manchester. $\times \frac{1}{3}$.

PLATE 28.

Festuca rubra subsp. *genuina* Hack. var. h. *arenaria*; showing stoloniferous habit. Charles Bailey Herbarium. $\times \frac{1}{3}$.

PLATE 29.

Festuca rubra subsp. *fallax*, showing caespitose habit. W. O. Howarth Herbarium. $\times \frac{1}{3}$.

PLATE 30.

Festuca juncifolia, showing general habit. Charles Bailey Herbarium, European Collection. $\times \frac{1}{3}$.

A Systematic and Ecological Account of a Collection of Blue-Green Algæ from Lahore and Simla*. By S. L. GHOSE, M.Sc. (Communicated by Prof. F. E. FRITCH, D.Sc., F.L.S.)

(PLATE 31.)

[Read 3rd May, 1923.]

INTRODUCTION.

PRACTICALLY no work has been done on the Myxophyceæ of India. With the exception of a few records of certain Indian species by Schmidle †, Turner ‡, West §, and Gomont ||, nothing is known about them. None seem to have been recorded from the Panjab Plains, and for this reason a systematic study of the blue-green algæ of certain localities in the Panjab was thought to be desirable. Accordingly, a collection of the Myxophyceæ from Lahore was made by the writer during the years 1917-19. A few specimens were also collected at Simla, which differs in climate and altitude from Lahore, with the object of making a comparison as to the time of their vegetative occurrence and spore-formation at the two stations. In these collections 41 species representing 23 genera were found, of which 9 species and 3 varieties are new.

Lahore is situated in latitude $31^{\circ} 35'$ N. and longitude $74^{\circ} 20'$ E. at a height of about 700 feet above the sea-level. The hottest months, namely May and June, have a mean maximum temperature of 106° F.; the highest temperature recorded being 120° F. The coldest months, namely December and January, have a mean minimum temperature of 40° F., the thermometer never falling below 29° F. The rainfall is confined chiefly to the months of July, August, and September, and ranges between 8 and 25 inches per annum.

Simla lies in latitude $31^{\circ} 6'$ N. and longitude $77^{\circ} 10'$ E., at an altitude of about 7,000 feet above sea-level. The mean temperature of January, the coldest month, is 40.6° F., and that of June, the warmest month, is 67.1° F.

* From the Botanical Department, East London College (University of London). Part of this work was done in the Government College Laboratory, Lahore, and in the Botany School, Cambridge.

† Schmidle in Hedwigia, xxxix. 1900, and Allg. bot. Zeitschr. vi. 1900.

‡ Turner, W. B., "Algæ aquæ dulcis Indiæ Orientalis," K. Vet.-Akad. Handl. xxv. Nr. 5, 1892.

§ West, W. and G. S., "Algæ of Burmah," in Ann. Roy. Bot. Gard., Calcutta, vi. 1907.

|| Gomont, M., in Bot. Tidsskrift, xxiv. 1901, p. 202.

The mean temperature of the whole year is 54·8° F. During the months of December to March snow may fall, and may lie for several weeks on the ground. The period of heaviest rainfall is from June to September with an average of 52 inches, while the average for the whole year is about 70 inches.

Blue-green algæ are met with at all times of the year in Lahore, but are most abundant after the rains, that is in the months of September, October, and November. Most of the Lahore Myxophyceæ are subaerial in habit, very few totally aquatic. This is due to the fact that there are no large permanent and stagnant sheets of water. The River Ravi, which flows at a distance of about three miles from the town, is too rapid to contain any free-floating blue-green algæ in great abundance. After the rains or during floods, small ponds and pools are produced, which contain a few planktonic forms, but these disappear during the summer as the water slowly evaporates.

After the rains a bluish-green slimy layer is generally formed on lawns and waste ground where water has stood for a short time. This is usually made up of species of *Glæocapsa* (*rupestris*, *conglomerata*, *quaternata*), *Aphanocapsa* (*biformis*), *Nostoc* (*muscorum*), *Anabæna* (*variabilis*, *gelatinicola*, sp. n.), and *Phormidium* (*autumnale*). If the soil is clayey, like that near the banks of the river, *Microcoleus vaginatus* is often found growing on it. Sometimes beautiful circular patches, woolly or slimy in appearance, are seen scattered on the surface of lawns. These expand and finally coalesce to produce a brownish-green stratum, which for the most part consists of *Campylonema lahorensis*, with which, however, species of *Glæocapsa* (*rupestris*, *conglomerata*), and *Anabæna* (*variabilis*) may be intermingled. In the drains and constantly wet places species of *Oscillatoria* (*tenuis*) and *Phormidium* (*autumnale*) may frequently occur throughout the year. Sometimes, especially in the months of September and October, *Symploca muralis* and *Cylindrospermum stagnale* are met with adhering to the damp sides of the drains above the water-level.

The aquatic blue-green algæ of Lahore are rarely free-floating. *Clathrocystis æruginosa*, species of *Arthrospira* (*platensis*, *spirulinoides*, sp. n.), *Lyngbya æstuarii*, and *Anabæna spiroides* var. *contracta* are the only forms found with this habit. Species of *Merismopedia* are occasionally met with, but are too infrequent for identification. Generally, the aquatic forms occur either on the surface of submerged plants or other objects, or adhering to the banks. Amongst the former are *Chroococcus turgidus*, species of *Microcystis* (*litoralis*, *Donnelli*), *Chamæsiphon filamentosa*, sp. n., and *Calothrix parietina*; amongst the latter species of *Oscillatoria* (*princeps* var. *pseudo-limosa* var. nov., *tenuis*), *Lyngbya* (*perelegans*), *Scytonema* (*Fritschii*, sp. n., *crispum*), and *Rivularia* (*natans*).

Certain subaerial forms have adopted a peculiar mode of life. Tree-trunks of *Acacia modesta* are commonly seen to be covered with a bluish-green

layer, which becomes very slimy and conspicuous after the rains, and consists of *Phormidium truncicolum*, sp. n., *Lyngbya truncicola*, sp. n., and *Tolypothrix campylonemoides*, sp. n., in rapid growth and multiplication. Hormogones are formed abundantly in the wet season, and, as the stratum dries, these produce mucilaginous sheaths, which slowly get thicker, firm, and coloured. The stratum then becomes thin and papery, and may ultimately peel off the trunk of the tree.

The type form of *Lyngbya circumcreta* is planktonic, while the new variety described below forms a gelatinous stratum on wet soil. Similarly, *Anabæna gelatinicola*, sp. n., whose nearest allies (*A. spiroides*, Klebahn., and *A. Flos-aquæ*, Bréb.) are both planktonic, occurs as a gelatinous stratum on moist bare ground. It is curious that both *Lyngbya circumcreta* var. *gelatinicola*, and *Anabæna gelatinicola*, sp. n., have spiral trichomes with many broad and closely arranged coils, thus differing from their free-floating allies.

The blue-green algæ of Lahore are exposed to the most extreme conditions during the months of May and June, when it is very hot and dry. At this time the cells or filaments are either enveloped by thick and coloured sheaths (as in species of *Gleocapsa*, *Campylonema*, and *Lyngbya*) or they produce resting spores (as in *Gleocapsa rupestris*, species of *Cylindrospermum*, *Aulosira*, *Nostoc*, *Anabæna*, and *Rivularia*). The threads of the subaerial species of *Oscillatoria* seem to be able to retain their vitality without the help of a sheath or spores. As soon as these dried filaments obtain access to moisture they form hormogones and multiply.

In Simla, where the rains occur earlier and are more frequent, slimy strata consisting mainly of species of *Gleocapsa* and *Anabæna* are formed on rocks throughout the months of July, August, and September, but as soon as the rains stop rapid spore-formation takes place. Thus, most of the *Cylindrospermum licheniforme* found in October was in spore condition, and vegetative stages could only be secured with great difficulty. Similarly, *Anabæna variabilis* was forming spores abundantly even in August. It seems, therefore, that spore-formation takes place earlier in Simla than in Lahore. This is probably to be ascribed to two causes, namely: first, the absence of standing water, the plants growing vegetatively on the rocks as long as rains last, and secondly, the severe winter, which follows the rainy season, and during which there is always a snowfall. Before the rains the rocks of Simla are quite bare of any algæ, but species of *Oscillatoria* and *Gleocapsa* may be found growing in drains and round water-taps, etc. Thus in Lahore the vegetative season for most Myxophyceæ seems to be between August and February, and the fruiting season between February and April, while in Simla the vegetative season is from June to October, and the fruiting season from September to November. In Simla the resting season is from November to April.

SYSTEMATIC ENUMERATION OF THE SPECIES OBSERVED.

CHROOCOCCACEÆ.

1. CHROOCOCCUS TURGIDUS (Kütz.), Näg., Gatt. einzell. Alg. 1849, p. 46.

Diam. cell. = 12–20 μ .

Hab. Lahore, in stagnant pools or ditches, generally adhering to the submerged parts of the tanks or to floating masses of decaying vegetable matter; found for the most part of the year.

2. GLÆOCAPSA RUPESTRIS, Kütz., Tab. Phycol. i. 1845–49, p. 17, pl. 22. fig. 2.

Diam. cell. = 3–6 μ .

Hab. Lahore, on moist ground, generally on lawns after a little rain or watering. It forms a thick, gelatinous green layer, which becomes greenish-brown when dry; most abundant during the rainy season.

3. GLÆOCAPSA CONGLOMERATA, Kütz. *op. cit.* p. 16, pl. 20. fig. 8.

Diam. cell. = 3–5 μ .

Hab. Lahore, on wet ground; most part of the year.

4. GLÆOCAPSA QUATERNATA (Bréb.), Kütz. *op. cit.* p. 15, pl. 20. fig. 1.

Diam. cell. = 3–4.5 μ .

Hab. Lahore, on moist ground after a little rain or watering; August–March.

5. APHANOCAPSA BIFORMIS, A. Br. in Rabenh. Alg. No. 2453.

Diam. cell. = 4–7 μ .

Hab. Lahore, on moist ground or banks of drains; August–March.

6. APHANOTHECE PALLIDA (Kütz.), Rabenh., Fl. Europ. Alg. ii. 1865, pp. 64–65.

Diam. cell. = 4 μ ; long. cell. = 6 μ .

Hab. Lahore, on bare moist ground; August–March.

7. MICROCYSTIS LITORALIS (Hansg.), Forti, in De Toni, Syll. Alg. v. 1907, pp. 89–90. (*Polycystis litoralis*, Hansg., in Foslie, Mar. Alg. of Norway, 1890, p. 169, pl. 3. fig. 3.)

Diam. cell. = 3 μ ; long. cell. = 5–7 μ .

Hab. Lahore, in tanks of the Shalamar Gardens, forming dirty green floating masses in association with other algæ; most of the year.

8. *MICROCYSTIS* DONNELLI, Wolle, in Bull. Torr. Bot. Club, vi. 1879, p. 282.

Diam. cell. = $3\ \mu$.

Hab. Lahore, in stagnant rain-water pools, mostly adhering to submerged objects, but sometimes free-floating; October–March.

9. *GLATHROCYSTIS* ÆRUGINOSA (Kütz.), Henfrey, in Micr. Journal, 1856, p. 53, pl. 4. figs. 28–36.

Diam. cell. = $3\text{--}4\ \mu$.

Hab. Lahore, on the surface of quiet stagnant water, forming a dirty green scum, which presents to the naked eye a finely granular appearance; October–March.

CHAMÆSIPHONACEÆ.

10. *CHAMÆSIPHON* FILAMENTOSA, sp. n. (Pl. 31. fig. 1.)

Plantis solitariis vel fasciculatis; gonidangiis maturis $4\text{--}6\ \mu$ crassis, usque ad $200\ \mu$ longis, filamentosis, basin versus in stipitem attenuatis; vaginis achrois; gonidiis numerosis, $5\text{--}6\ \mu$ crassis, doliformibus, protoplasmate granuloso.

Hab. Lahore, in a stagnant pool of water in the Botanical Gardens, growing on a species of *Pithophora*; October 1918.

This species resembles *C. conferricola*, A. Br., but differs from it in two respects: first, the gonidangia are very long (up to $200\ \mu$) and filamentous, whilst even in *C. conferricola* var. *elongata* Rab. they are only $22\ \mu$ long; secondly, the gonidia are barrel-shaped, while in *C. conferricola* they are shorter than long or seldom quadrate.

OSCILLATORIACEÆ.

11. *OSCILLATORIA* PRINCEPS, Vauch.; Gomont, Monogr. Oscill. 1893, p. 226, pl. 6. fig. 9; var. *PSEUDO-LIMOSA*, var. nov. (Pl. 31. fig. 2.)

Strato obscure æruginoso; trichomatibus rectis, rigidis, flavo-viridibus, siccitate fragilibus, non-torulosis, $31\text{--}35\ \mu$ crassis; articulis brevissimis, protoplasmate granuloso; apicibus plerumque hand attenuatis et vulgo rectis; cellula apicali superne leviter convexa; calyptra nulla; dissepimentis non-granulatis.

Hab. Lahore, in a slow-flowing dirty drain, at first attached to the mud, then free-floating; found only once, in September, 1918, in spite of all efforts to find it again.

This variety differs from the typical form of the species in not having a clearly tapering and curved apex. The majority of the filaments have a straight broad apex like that of *O. limosa*, Ag., to which, however, I do not refer this alga because of its much greater thickness and the absence of any granulation at the transverse walls. Boergesen (Freshwater Algæ of the

Faeroes, 1901, p. 208) has recorded *O. limosa* up to $33\ \mu$ thick, but unfortunately he does not figure his form. There are two other reasons which induce me to refer this alga to the species *princeps* rather than to *limosa*. Firstly, among Prof. G. S. West's figures of *O. princeps* at the British Museum (Natural History), London, there are two in which the apex is quite straight as in the alga under discussion. Secondly, filaments are sometimes seen in my material, which show a slight curvature and attenuation at the apex (Pl. 31. fig. 2, b).

12. *OSCILLATORIA TENUIS*, Agardh; Gom., Monog. Oscill. 1893, p. 240, pl. 7. figs. 2, 3.

Diam. cell. = $5-9\ \mu$.

Hab. Lahore, commonly found in dirty drains and in places constantly wet, such as on mud round water-pipes or wells; throughout the year.

13. *PHORMIDIUM AUTUMNALE* (Agardh), Gom. *tom. cit.* p. 207, pl. 5. figs. 23, 24.

Diam. cell. = $4-7\ \mu$.

Hab. Lahore, in drains or on moist ground; most of the year.

14. *PHORMIDIUM TRUNCICOLA*, sp. n. (Pl. 31. fig. 3.)

Strato valde expanso, membranaceo, flavo-viride vel æruginoso; vaginis diffuentis, fibrosis; trichomatibus $6-8\ \mu$ crassis, subparallelis, ad genicula distincte constrictis; articulis fere tam longis quam latis; apicibus attenuatis; calyptra nulla; contentu in media cellularum densioro.

Hab. Lahore, growing on trunks of *Acacia modesta*, associated with other blue-green algæ; July–October.

This species is like *P. fragile* (Menegh.), Gom., but differs from it in its peculiar habitat, its much broader filaments, and in the nature of the stratum.

15. *ARTHROSPIRA PLATENSIS* (Nordst.), Gom. *tom. cit.* p. 247, pl. 7. fig. 27.

Diam. spir. = $25-30\ \mu$; dist. inter anfractibus = $40-55\ \mu$; diam. cell. = $6-8\ \mu$.

Hab. Lahore, free-floating in stagnant water, generally associated with *Clathrocystis æruginosa*; most of the year.

16. *ARTHROSPIRA SPIRULINOIDES*, sp. n. (Pl. 31. fig. 4.)

Trichomatibus ærugineis; articulis haud constrictis, $5-6\ \mu$ latis, $4-12\ \mu$ longis, protoplasmate subtiliter granuloso; spiris densis anfractibus contiguis, rectis vel leviter flexilibus, usque ad $60\ \mu$ longis; diametro $12-15\ \mu$.

Hab. Lahore, in a dirty stagnant rain-water pool, free-floating; October, 1918.

This alga looks very much like a *Spirulina*, such as *S. subsalsa*, Oerst., but because it shows some clear dissepiments, it cannot be referred to that unicellular genus.

17. *LYNGBYA ÆSTUARII* (Mert.), Liebm., Gom. Monog. Oscill. 1893, p. 127, pl. 3. figs. 1, 2.

Diam. fil. = 13–16 μ ; diam. trich. = 10–13 μ .

Hab. Lahore, free-floating in a stagnant pool, intermingled with other algæ ; September 1918.

18. *LYNGBYA PERELEGANS*, Lemm., Abh. Nat. Ver. Brem. xvi. 1906, p. 355 ; xviii. p. 153, pl. 11. figs. 13, 14.

Diam. fil. = 1.5–2 μ ; diam. cell. = 1–1.5 μ ; long. cell. = 2–8 μ .

Hab. Lahore, adhering to the walls or to the submerged objects in the tanks of the Shalamar Gardens ; most of the year.

19. *LYNGBYA KASHYAPI**, sp. n. (Pl. 31, fig. 5.)

Strato expanso, obscure purpureo ; filamentis curvatis, densissime intricatis ; vaginis firmis, crassis, obscure cæruleis vel purpureis, lævibus, chitinosi ; trichomatibus tenuibus, ad genicula non-constrictis, 3–4 μ crassis ; articulis quadratis, diametro brevioribus, protoplasmate grosse granuloso ; dissepimentis haud granulosis, sæpe obliquis vel curvatis ; apicibus rotundatis, non-capitatis ; calyptra nulla.

Hab. Lahore, on moist ground which has been under water for some time, such as the drying tanks of the Shalamar Gardens ; August–April.

This species resembles *L. versicolor* (Wartm.), Gom. and *L. ærugineo-cærulea* (Kütz.), Gom., but it differs from them in the colour of the stratum, in the coloured sheaths, and in the oblique or curved septa ; from the former it differs in the nature of the apex.

20. *LYNGBYA TRUNCICOLA*, sp. n. (Pl. 31, fig. 6.)

Strato tenui, expanso, obscure æruginoso ; filamentis rectis, plus minusve parallelis, 14–16 μ crassis ; vaginis primum hyalinis et tenuibus deinde fuscis et firmissimis, non-lamellosis ; trichomatibus ærugineis, 12–14 μ crassis, ad genicula haud constrictis ; articulis brevissimis, 3–4 μ longis, protoplasmate granuloso ; apicibus rotundatis, haud attenuatis ; calyptra nulla ; dissepimentis non-granulatis.

Hab. Lahore, on trunks of *Acacia modesta*, forming a thin stratum in association with *Phormidium truncicola* and *Tolypothrix campylonemoides* ; July–October.

This species resembles *L. æstuarii* very much in size and general appearance under the microscope, but differs from it in its peculiar habit, its non-attenuated apex, in having no calyptra, and in the non-lamellose sheath, though the latter is very firm when old.

* This species is named after my esteemed teacher, Professor S. R. Kashyap, M.Sc., B.A. (Cantab.), of the Government College, Lahore.

21. *LYNGBYA CIRCUMCRETA*, G. S. West, Journ. Linn. Soc. London, xxxviii. 1907, p. 174, pl. 9. fig. 7; var. *GELATINICOLA*, var. nov. (Pl. 31. fig. 7.)

Strato sordide æruginoso; filamentis in muco nidulantibus, in spiram contortis, spiris usque ad $100\ \mu$ latis et interdum cum anfractibus 20 vel pluribus; vaginis tenuissimis; trichomatibus angustis, circa $1\ \mu$ crassis, fragilibus, æruginosis; articulis subquadratis, plerumque diametro brevioribus; dissepimentis sæpe distinctis; apicibus rotundo-truncatis.

Hab. Lahore, occurring in a gelatinous stratum, adhering to the walls of drains, along with species of *Closterium*; October 1919.

This variety differs from the type in its non-planktonic habit and its much broader spirals with more numerous coils.

22. *SYMPLOCA MURALIS*, Kütz.; Gom., Monog. Oscill. 1893, p. 112, pl. 2. fig. 10.

Alt. fasc.= ad 3 mm.; diam. trich.= $3.5-4\ \mu$.

Hab. Lahore, on damp walls of drains; November 1919.

23. *SYMPLOCA MUSCORUM* (Ag.), Gom. *tom. cit.* p. 110, pl. 2. fig. 9.

Alt. fasc.= ad 7 mm.; diam. trich.= $5-6\ \mu$.

Hab. Simla, on wet rocks or damp exposed roots of trees; August-October.

24. *MICROCOLEUS VAGINATUS* (Vauch.), Gom. *tom. cit.* p. 355, pl. 14. fig. 12.

Diam. trich.= circa $5\ \mu$.

Hab. Lahore, commonly occurring on moist ground, generally on clayey soil, also on the soil in flower-pots; most of the year.

25. *MICROCOLEUS CHTHONOPLASTES*, Thuret; Gom. *tom. cit.* p. 353, pl. 14, figs. 5-8.

Diam. trich.= circa $3\ \mu$.

Hab. Lahore, on moist ground; March 1919.

In my material there were relatively few threads in the bundle, which probably marks a young condition. In other respects the alga is quite typical. The existence of saltpetre in the soil of Lahore is probably responsible for the presence of this species, which is mainly found in marine or brackish habitats.

NOSTOCACEÆ.

26. *NOSTOC MUSCORUM*, Agardh; Born. & Flah., Revis. des Nostoc., in Ann. Sci. Nat. Bot. sér. VII., vii. 1888, p. 200.

Diam. cell.= $4.5-5\ \mu$; long. cell.= $5-7\ \mu$; diam. heterocyst.= $6-7\ \mu$; diam. spor.= $4-8\ \mu$; long. spor.= $7-10\ \mu$.

Hab. Lahore, on moist ground, generally intermingled with species of *Glæocapsa*; August-March.

27. *ANABÆNA VARIABILIS*, Kütz. ; Born & Flah. *op. cit.* p. 226.

Diam. cell. = 4–5 μ ; diam. spor. = 8–12 μ .

Hab. Lahore, on moist ground. It occurs most abundantly during the months February to April. Spores are formed in March and April. At Simla it was collected, with ripe spores, in the month of September, adhering to damp rocks.

28. *ANABÆNA SPIROIDES*, Klebahn, var. *CONTRACTA*, Klebahn, in *Flora* 1895, p. 29, pl. 4. figs. 14, 15.

Diam. spir. = ad 20 μ ; diam. trich. = 5–7 μ .

Hab. Lahore, free-floating in stagnant water, generally associated with *Clathrocystis aruginosa* ; October–March.

Heterocysts were rare and no spores were observed.

29. *ANABÆNA GELATINICOLA*, sp. n. (Pl. 31. fig. 8.)

Strato crasso, gelatinoso ; trichomatibus plerumque solitariis, in spiram contortis interdum in partes rectas transientibus ; articulis sub-sphaericis, 6–7.5 μ crassis, apicibus acutis, protoplasmate granuloso ; heterocystis 7–8 μ crassis, globosis ; sporis in seriebus dispositis ab heterocystis remotis, sphaericis, circa 11 μ diametro.

Hab. Lahore, on moist ground ; September–March.

This species resembles *A. spiroides* and *A. Flos-aquæ* (Lyngb.), Bréb. in having spirally twisted trichomes, but differs from them in two important respects. First, it is not planktonic like these two species ; secondly, the spirals are densely arranged, so that the trichome generally presents a coiled and not a corkscrew-like appearance. In *A. Flos-aquæ*, var. *circularis*, G. S. West, the trichomes are, however, coiled, but make only 1–1½ turns, while in the present species there may be as many as ten turns lying in one horizontal plane. Moreover, *A. gelatinicola* differs from *A. Flos-aquæ* in having spherical and not elongated spores.

30. *CYLINDROSPERMUM STAGNALE* (Kütz.), Born. & Flah. *op. cit.* p. 250.

Diam. trich. = 4–5 μ ; diam. heter. cyst. = 6–7 μ ; long. heterocyst. = ad 11 μ ; diam. spor. = 10–14 μ ; long. spor. = ad 35 μ .

Hab. Lahore, on moist soil, constantly wetted, such as that round water-pipes and drains ; September–March.

31. *CYLINDROSPERMUM LICHENIFORME* (Bory), Kütz. ; Born. & Flah. *op. cit.* p. 253.

Diam. trich. = 4 μ ; diam. heterocyst. = 5–6 μ ; long. heterocyst. = 7–10 μ ; diam. spor. = 12–14 μ ; long. spor. = ad 40 μ .

Hab. Simla, on moist sheltered rocks ; August and September 1919.

32. *AULOSIRA FERTILISSIMA*, sp. n. (Pl. 31. fig. 9.)

Strato expanso, sordide aeruginoso, membranaceo; trichomatibus rectis vel leviter flexuosis, parallelis vel dense intricatis, raro pseudo-ramosis; cellulis 6–11 μ latis et 7–10 μ longis, in statu juvenali cylindricis denique doliformibus, protoplasmate granuloso; vaginis crassis, primum gelatinosis et hyalinis deinde firmis et fuscescentibus; heterocystis intercalaribus, oblongis vel ellipticis, 8–9 μ latis et 10–14 μ longis, contentu homogeno; sporis in catenis longis dispositis cum cellulis moribundis deplanatis alternantibus, plerumque oblongo-ellipticis interdum propter compressionem angulosis, dimensione 18–24 $\mu \times$ 11–13 μ ; epispора plerumque firma lævi, interdum fusca.

Hab. Lahore, in one of the broad water-courses of the Shalamar Gardens, on decaying leaves of *Nelumbium speciosum*; October–March.

There are two features peculiar to this species. First, at the time of reproduction the whole of the trichome becomes fertile and the cell or cells situated between the spores either slowly die off or become changed into dark-green biconcave cells. A fertile filament then consists of spores, between which dead coloured discs are seen. This resembles what has been figured by Borzi in connection with spore-formation in *Tolypothrix Wartmannia* Rabh. (Nuovo Giorn. Bot. Ital., xi. 1879, pl. 10. fig. 15, copied in my figure, Pl. 31. fig. 10). Secondly, in rare cases the filaments are seen to produce very short pseudo-branches, resembling those of *Plectonema*, which, however, does not possess any heterocysts. At a level with one of the concave cells the mucilage sheath swells up and one part of the filament grows out into a short pseudo-branch (Pl. 31. fig. 9, b, e). The alga cannot be referred to *Tolypothrix* because there is no heterocyst at the point of ramification, nor to *Scytonema*, as the branches are always single. For the present the alga seems to find its best place in the genus *Aulosira* in spite of the occasional ramification, but investigation of further material may show that it is a peculiar stage of an alga like *Tolypothrix* (which is sometimes very little branched) or a distinct genus.

33. *MICROCHÆTE CALOTRICHOIDES*, Hansg., in Beihefte z. Bot. Centralbl., xviii. p. 494.

Diam. fil. = 8–12 μ ; diam. trich. = 6 μ ; diam. heterocyst. = 6 μ ; long. heterocyst. = 7–8 μ .

Hab. Lahore, adhering to the surface of submerged leaves in a stagnant pool of water, intermingled with *Edogonium* and other algæ; October–March.

SCYTONEMATACEÆ.

34. *SCYTONEMA FRITCHII**, sp. n. (Pl. 31. fig. 11.)

Strato floccoso, viride-fusco; filamentis tenuibus, elongatis, 15–20 μ crassis; trichomatibus 7–8 μ crassis, articulis plerumque latitudine duplo longioribus;

* This species is named after Prof. F. E. Fritch, D.Sc., of the East London College, whose generous help was very valuable to me during this piece of work.

dissepimentis distinctis, protoplasmate granuloso; pseudo-ramis plerumque geminatis, remotis, tam latis quam filamentis primariis; vaginis firmis, interdum constrictis, lamellosis, lamellis parallelis, hyalinis; heterocystis intercalariis, pellucidis, diametro $18-22\ \mu$, solitariis et cylindricis, usque ad $35\ \mu$ longis, vel 2-4 in seriebus et quadratis.

Hab. Lahore, adhering to the submerged sides of the tanks of the Shalamar Gardens; most of the year.

This species resembles *S. amplum*, W. West & G. S. West, but in the latter the sheath is differentiated into two parts, the pseudo-branches are narrower than the main filaments, and the trichomes are thinner than those of the former.

35. *SCYTONEMA CRISPUM* (Ag.), Born., in Bull. Soc. Bot. de France, xxxvi. 1889, p. 156.

Diam. fil. = $20-30\ \mu$; diam. trich. = $14-20\ \mu$.

Hab. Lahore, in one of the tanks of the Shalamar Gardens, adhering to the submerged walls; most of the year.

36. *SCYTONEMA VARIUM*, Kütz.; Born. & Flah. *op. cit.* p. 97.

Diam. fil. = $10-17\ \mu$; diam. trich. = $6-8\ \mu$.

Hab. Lahore, on the surface of damp flower-pots and on damp soil intermingled with moss; August-March.

37. *CAMPYLONEMA LAHORENSE*, Ghose, in 'New Phytologist,' xix. 1920, p. 35, figs. 1-6.

Strato terrestre, floccoso, læte æruginoso vel cæruleo-fusco, pro parte in limo nidulanti vaginis inconspicuis tenuibus et hyalinis, pro parte emerso vaginis firmis arcuatis crassis lamellosis brunneis; filamentis plus minusve in hemicyclum curvatis, usque ad $1-1\frac{1}{4}$ mm. longis; trichomatibus æruginis, $6-9\ \mu$ crassis, ad genicula leviter constrictis, raro pseudo-ramosis, pseudo-rami solitariis vel geminatis; cellulis tam latis quam longis vel diametro paullo longioribus vel brevioribus, protoplasmate grosse granuloso; dissepimentis ægre conspicuis in filamentis maturis; heterocystis in media filamenti vel passim per totam longitudinem filamenti dispersis, haud ramis contiguis, rectangularis vel ellipsoideis, $12-21\ \mu$ longis et $7-9\ \mu$ latis; sporis $7-11\ \mu$ longis et $5-7\ \mu$ latis, in seriebus intra vaginam dispositis; epispora brunnea, crassa et lævi.

Hab. Lahore, on damp lawns and waste ground; August-March.

The genus *Campylonema* was established by Schmidle in 1900 (*Hedwigia*, xxxix. p. 181) to include his species *C. indicum* (syn. *Stigonema indica*, Schm.), which was collected at Bombay. This species was epiphytic on Hepaticæ, and it shows a combination of the characters of three genera (*Stigonema*, *Tolypothrix*, and *Scytonema*) as far as its branching is concerned. True branches are produced as in *Stigonema*, but there are likewise very rare false

branches, which may arise singly at the base of an heterocyst as in *Tolypothrix* or in pairs as in *Scytonema*. In addition to the points of distinction between it and the species under discussion already mentioned in my earlier paper (*loc. cit.* p. 38), another great difference lies in the absence of true branches in *C. lahorensis*, although a thorough search for them has been instituted. In view of this fact, *C. lahorensis* can hardly be included in the Stigonemataceæ, which are characterised by their true branching, but should rather be referred to the Scytonemataceæ, as Forti (in De Toni, Syll. Alg. v. p. 540) has already done for Schmidle's species. Whether this last is justified is, however, doubtful, since according to Schmidle's description and figures (*loc. cit.*) the bulk of the branching is true. A re-investigation of *C. indicum* is much to be desired. Should the true branching prove to be a regular and frequent feature, the species here described will have to be referred to a distinct genus of the Scytonemataceæ. A marked point of resemblance to Schmidle's form lies in the *Camptothrix*-like growth of the curved filaments with median heterocysts in *C. lahorensis*. This and the occurrence of both single and geminate branches are at present the chief grounds for referring the two species to the same genus.

38. TOLYPOTHRIX CAMPYLONEMOIDES, sp. n. (Pl. 31. fig. 12.)

Strato obscure cæruleo-fusco, tenui papyraceo; filamentis curvatis, 10–12 μ crassis; pseudo-ramis irregularibus, sparsis, brevibus, erecto-patentibus, solitariis vel raro geminatis; vaginis tenuibus; fragilibus, in statu juvenali achrois deinde luteis vel fuscis; trichomatibus 8–10 μ crassis, torulosis; articulis diametro brevioribus, protoplasmate granuloso; heterocystis solitariis, terminalibus vel intercalaribus, subglobosis, circa 11 μ latis et 9.5 μ longis.

Hab. Lahore, on trunks of *Acacia modesta*, associated with many other blue-green algæ, during the months of August to October.

In dry weather the stratum resembles a thin scaly bark, but after a little rain it becomes slimy and numerous hormogonia glide out of their sheaths. Some of these hormogonia are only one- or two-celled. If the weather remains moist and favourable, these hormogonia show active growth and form a delicate stratum by arranging themselves parallel to one another. They slowly secrete a sheath, which is at first very delicate and hyaline, but as the weather becomes drier, acquires a firmer character and takes on a yellowish-brown colour. At the same time the surface filaments become crescentic in shape owing to the two ends curving upwards. Heterocysts may arise in very young filaments or in mature ones. Pseudo-branches are few and are produced in connection with the heterocysts or in relation to the formation of concave discs. They are single or rarely geminate. In summer the filaments break up into many pieces, which may separate as sheathed "pseudo-hormogonia," resembling those mentioned by Schmidle in *Hedwigia*, xxxix. 1900, p. 181, in *Campylonema indicum*, (Pl. 31. fig. 12, b.)

This species shows intermediate characters between *Campylonema lahorensis* and *Tolypothrix*. It resembles the former in the crescentic shape of the filaments, in having single or geminate pseudo-branches, which may or may not be related to the heterocysts, but it differs from it in having no median heterocysts and in its preponderant *Tolypothrix*-like branching.

39. *TOLYPOTHRIX CONGLUTINATA*, Borzi, in Nuov. Giorn. Bot. Ital. xi. 1879, p. 371; Fritsch, Rep. National Antarctic Expedition, Natural History, vi. 1912, p. 38, pl. 3. figs. 145, 146; var. *COLORATA*, var. nov. (Pl. 31. fig. 13.)

Stratum primum æruginoso, deinde obscure fusco-viride, floccoso et tomentoso; filamentis irregulariter et dense intricatis, trichomatibus æruginis, 7-9 μ crassis, ad genicula constrictis; cellulis diametro brevioribus, protoplasmate granuloso; pseudo-ramis multis, brevis et flexuosis, solitariis vel raro geminatis; vaginis crassis, asperulis, primum achrois, deinde luteo-fuscis; heterocystis solitariis, globosis sed leviter deplanatis, circa 8 μ diametro.

Hab. Simla, on damp rocks and moist exposed roots of trees; August 1919.

This variety differs from the type mainly in having a coloured sheath in older filaments. Moreover, its stratum is felt-like and not gelatinous-crustaceous, like that of the type. The heterocysts, which are often paired, are not quite spherical, but in most cases distinctly drawn out in the transverse direction.

RIVULARIACEÆ.

40. *CALOTHRIX PARIETINA* (Näg.), Thur.; Born. & Flah. in Ann. Sci. Nat. Bot. sér. VII., vii. 1886, p. 366.

Diam. fil. ad bas. = 10-12 μ ; diam. trich. ad bas. = 8-10 μ ; diam. heterocyst. = 8 μ ; crass. parietis vaginæ = 1.5 μ .

Hab. Lahore, in stagnant rain-water pools, adhering to submerged leaves in association with species of *Edogonium*; October-March.

41. *RIVULARIA NATANS* (Hedw.) Welwitsch; Born. & Flah. *op. cit.* 1886, p. 369. (*Glæotrichia natans*, Rabenh. Deutschl. Kryptogamenfl. 1847, p. 90.)

Diam. trich. ad bas. = 9-10 μ ; diam. tegument. = ad 40 μ ; diam. spor. = 18-24 μ ; long. spor. = 60-70 μ .

Hab. Lahore, in small pools near the River Ravi, the colonies generally adhering to the sides, sometimes free-floating; October-March.

CONCLUSION.

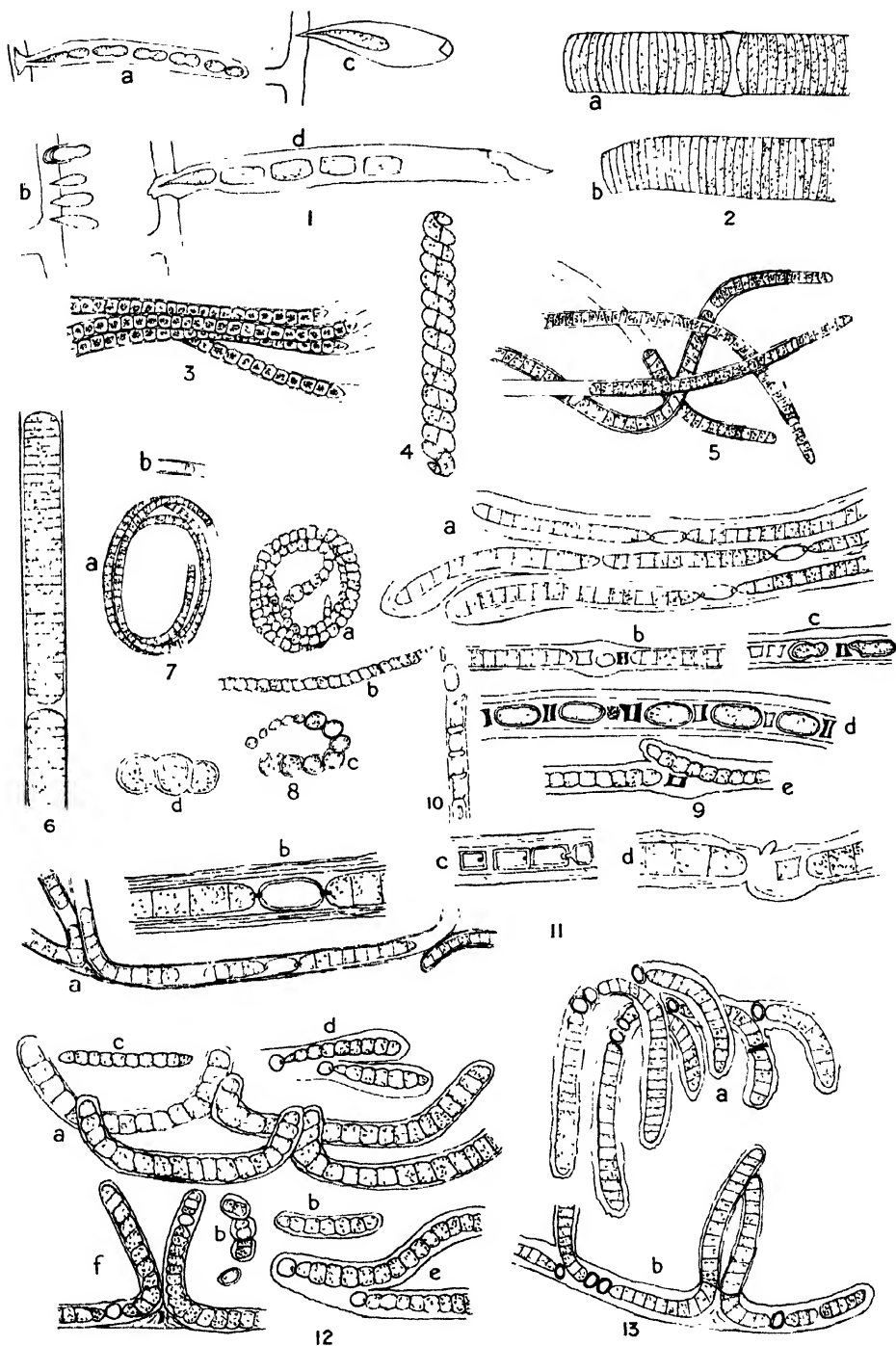
In conclusion, I have much pleasure in expressing my heart felt thanks to Dr. F. E. Fritsch, Professor of Botany, East London College, for generous help and guidance during the preparation of this paper. Without his help it

would have been impossible to publish it in the present form. To Professor S. R. Kashyap of the Government College, Lahore, I am indebted for many suggestions and for the keen interest which he took in connection with this work, while I was in India.

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EXPLANATION OF PLATE 31.

- Fig. 1. *Chamæsisiphon filamentosa*, sp. n., different stages of gonidium-formation. (*a*, $\times 350$; *b*, *c*, *d*, $\times 700$.)
- Fig. 2. *Oscillatoria princeps*, Vauch., var. *pseudo-limosa*, var. nov. *a*, apical portion of an ordinary thread; *b*, a slightly curved and tapering apex. ($\times 250$.)
- Fig. 3. *Phormidium truncicola*, sp. n., a portion of the stratum. ($\times 350$.)
- Fig. 4. *Arthrospira spirulinoides*, sp. n. ($\times 350$.)
- Fig. 5. *Lyngbya Kashyapii*, sp. n. ($\times 350$.)
- Fig. 6. *Lyngbya truncicola*, sp. n., portion of a filament. ($\times 420$.)
- Fig. 7. *Lyngbya circumcreta*, G. S. West, var. *gelatinicola*, var. nov. *a*, a single filament; *b*, apex. ($\times 840$.)
- Fig. 8. *Anabaena gelatinicola*, sp. n. *a*, a coiled and *b*, a young straight filament; *c*, spore-formation; *d*, mature spores. ($\times 350$.)
- Fig. 9. *Aulosira fertilissima*, sp. n. *a*, vegetative filaments; *b*, *c*, pseudo-branching; *c*, germination of a spore while in the filament; *d*, mature spores separated by biconcave cells. ($\times 350$.)
- Fig. 10. *Tolypothrix Wartmanniana*, Rabenh., portion of a filament with spores and intercalary cells. (After Borzi, $\times 210$.)
- Fig. 11. *Scytonema Fritschii*, sp. n. *a*, filaments showing pseudo-branching; *b*, single heterocyst; *c*, four heterocysts in a series; *d*, constricted sheath. (*a*, $\times 85$; *b*, *c*, *d*, $\times 350$.)
- Fig. 12. *Tolypothrix campylonemoides*, sp. n. *a*, curved filaments; *b*, sheathed "pseudo-hormogonia"; *c*, a young hormogone which has emerged from the sheath; *d*, *e*, single pseudo-branching; *f*, geminate pseudo-branching. ($\times 250$.)
- Fig. 13. *Tolypothrix conglutinata*, Borzi, var. *colorata*, var. nov. *a*, richly branched filaments; *b*, geminate pseudo-branching. ($\times 250$.)



BLUE-GREEN ALGÆ FROM INDIA

On New Species of Permian Osmundaceæ. By M. D. ZALESSKY.
(Communicated by Prof. A. C. SEWARD, F.R.S., F.L.S., Pres.G.S.)

(PLATES 32-34.)

[Read 29th November, 1923.]

BEFORE describing the new species of Osmundaceæ found in the Permian rocks of the Ural Mountains, I shall begin with an account of the stele of *Bathypteris rhomboidalis* which I discovered in a specimen belonging to the University of Kazan sent to me for study by the late Prof. Krotov.

The stele of this fern was not previously known because a specimen which was described by Dr. Kidston and the late Prof. Gwynne-Vaughan, and was formerly in the hands of Kutorga and Eichwald, shows only the outer part of the stem which is covered by crowded petioles. In spite of the bad preservation of the stele in the Kazan specimen, the tissue of which is for the most part in a much worse state of preservation than in the Petrograd specimen, I have been able to make out the salient structural features. Although the diameter of the Kazan specimen reaches 95 mm. its stele is only 6·5 mm. in diameter. The stele consists of two kinds of xylem elements, narrower tracheids at the periphery, and wider elements in the centre; both kinds of xylem elements have transversely elongated pits like those in the tracheids of *Zalesskya* and *Thamnopteris*. It is unfortunate that the stele is rather crushed and broken by radial cracks into a series of cuneiform portions which become narrower towards the centre; the elements are much compressed tangentially (Pl. 33. fig. 6). Between these deformed cuneiform pieces of xylem one sees the tracheids of the inner xylem which occupy the remainder of the stele. The phloem is preserved in some places as a brown tissue abutting on the xylem. Its structure is difficult to determine. The xylem bundles of the leaf-trace, as seen in this region, are oval in outline (Pl. 33. fig. 7). The protoxylem elements are found on the adaxial side of the bundle. Occasionally at the periphery of the vascular cylinder one sees the vascular bundles of roots passing out at a wide angle. The inner cortex, preserved in some places, consists of parenchymatous cells, sometimes elongated and with more or less sinuous cell-walls. The inner cortex, in which cavities occur marking the position of leaf-traces, is crossed in all directions by roots, oblique and longitudinal sections of which are met with in the middle of this tissue.

THAMNOPTERIS *Brongniart*, 1849.

(Tableaux des genres de Végétaux fossiles, p. 35.)

THAMNOPTERIS *KIDSTONI* *Zalessky*, n. sp. (Pl. 32; Pl. 34. figs. 6 & 7.)

The transverse section of the specimen from the Permian rocks of the Urals (probably from the mine Kirmensky: the specimen is in the possession of my son, George Zalessky) shows that this fern has a central stele about 11.5 mm. in diameter; the xylem, about 10 mm. in diameter, consists of two distinct regions, an inner and an outer. The inner region is occupied by xylem elements wider and shorter than those in the outer region, the elements of which present the appearance of normal xylem tracheids. The more central elements constitute the greater part of the xylem mass, forming a column about 7.5 mm. in diameter; the outer ring of the xylem is about 2 mm. in breadth (Pl. 32. figs. 2 & 3).

The outline of the periphery of the whole of the xylem mass is somewhat irregular because of the occurrence of prominences at the points of departure of leaf-traces which leave the stele at an angle of about 10° . In the inner xylem is a cavity due to the destruction of the more internal tissue. All the preparations show cells of parenchyma along the edge of this cavity, and these are associated in the central part with xylem tracheids. In order to make out the distribution of the cells of the parenchymatous tissue in the middle of the xylem elements, I prepared one transverse section of the stem from the lower part of the specimen where there is no cavity in the centre (Pl. 34. figs. 6 & 7). A cavity was found in most of the sections which were cut from the upper part of the specimen. The transverse section shows that the xylem cylinder of the stele in the lower part of the specimen reaches a diameter of 11 mm. The annular zone of the outer xylem is about 2 mm. broad; it surrounds a ring of the same breadth consisting of wider and shorter xylem elements, next to which is a narrow zone of parenchymatous cells of irregular form distributed in groups among the wider xylem elements. This zone appears as a brown border because its cells are darker in colour than the xylem elements which extend as far as the centre of the interrupted zone of parenchyma. The parenchymatous cells occupy only a limited space among the elements of the inner xylem and are distributed in groups, thus marking off a central part of the stele which is composed exclusively of wide xylem elements. The boundary of the central cavity to which reference has been made is situated in this zone of parenchyma, a fact which explains the occurrence of parenchymatous cells here and there on the edge of the cavity. There is no doubt that the cavity owes its origin to a line of weakness caused by the junction of the central part of the inner xylem with the peripheral portion where there occur groups of parenchymatous cells.

The broad zone of the inner parenchymatous cortex, which reaches a diameter of about 6 mm., surrounds the stele. Outside the parenchymatous cortex is a zone of sclerotic tissue the coloured thick-walled cells of which

mark the boundary between the inner and outer cortex. The stem up to this boundary has a radius of about 21 mm. ; the outer cortex occupies a small space, so that the stem as a whole does not exceed 46 mm. in diameter. The rest of the specimen is composed of petiole-bases investing the stem and closely pressed against it : of these, only the most internal are preserved ; the more external petiole-bases are shown in another specimen of the fern, which consists entirely of a group of these organs.

The elements of the outer xylem zone are sharply-pointed tracheæ with regularly disposed pits which are elongated in the direction of the breadth of the tracheæ and are disposed according to their size in two, three, or four vertical series ; some portions of the tracheal wall show pits in five or even six series. By their transversely elongated pits the xylem elements remind one of the scalariform tracheæ which have a single series of transversely elongated pits. The narrow protoxylem elements, in which the pits are uniseriate, exhibit a specially close resemblance to scalariform tracheæ. These protoxylem elements form a part of the outer xylem zone, chiefly in the prominences which mark the points of departure of the leaf-traces where the elements are grouped together at some distance from the edge of the prominences among the metaxylem tracheids. The remaining part of the outer xylem zone does not show much decrease in the tracheæ, which remain fairly constant from the centre to the periphery. The inner xylem, in contrast to the outer xylem, is composed of short and wide tracheæ which resemble irregular sacs tapering at the ends, with the result that the boundary between two kinds of xylem is obvious in the transverse sections and especially so in longitudinal sections. The tracheæ of the inner xylem have thinner walls than the elements of the more external xylem. The pits in their walls are transversely elongated, but their irregularity of distribution gives to the xylem elements the appearance of reticulate rather than scalariform vessels. This reticulate structure of the wall is noticeable not only in longitudinal but also in transverse sections, because the pits cover both the transverse and longitudinal walls of the tracheæ. All the elements of the xylem, both outer and inner, appear to be vessels, but the pits, because of the absence of the middle lamella in the walls, appear to be true pores. In the reticulate tracheæ each pit represents an independent perforation in the wall, but in the elements of the outer xylem zone all the pits of the same series communicate with one another by a split in the cell-wall, as in recent Osmundaceæ. The cell-wall of the tracheæ of *Thamnopteris Kidstoni* is preserved in such a way that the spaces in it are visible as double black lines in the middle part of the membrane, but the wall itself appears to be stained a brownish-yellow colour. The central portion of the stele, as I have already said, has a cavity along the border of which, and in contact with the short tracheæ of the inner xylem, as shown in longitudinal section, one can see here and there groups of isodiametric and rather small cells which have the characters of parenchyma, and undoubtedly represent the beginning of

the pith in the form of islands among the xylem elements which occupy the stele up to the centre. Groups of such cells were also discovered along the edge of the cavity in the transverse section of the stem. Outside the outer zone of the xylem there are from four to seven layers of small, thin-walled cells which represent the xylem-sheath (Pl. 32. fig. 2). In this sheath at a distance of one row of cells from the xylem are disposed here and there, in one or two layers, cells with brown contents which were no doubt specialized cells, because identical cells with brown contents are found in the xylem-sheath of the leaf-traces. The sheath is surrounded by a zone of phloem consisting of thin-walled, comparatively large cells which appear to be sieve-tubes. These sieve-tubes form a band of three or four layers. In some places the zone of sieve-tubes reaches a width of seven cells: this occurs on the sides of the xylem prominences where the phloem tissue, in consequence of the junction of the descending leaf-traces with the xylem of the stem, is removed from its normal position. The sieve-tubes are connected with the small-celled tissue which surrounds the whole stele by a zone of three to four layers of cells.

In some places, it is true, the number of rows is greater, being sometimes as many as eight. This zone certainly appears to be pericyclic; but it is not possible, in spite of the wonderful preservation of the tissue, to distinguish a peripheral series of cells having the structure of endodermis. This pericyclic zone comes out very clearly, being limited towards the centre by larger sieve-tubes and towards the periphery by no less large but thicker-walled cells of the inner cortex which in this region have black contents. The pericycle zone is equally clear in longitudinal section, because its cells have a somewhat prosenchymatous character and are easily distinguished from the isodiametric, empty cells of the inner cortex and the long and comparatively empty sieve-tubes which are clearly contrasted with the narrower and shorter cells of the xylem-sheath. The cells of the pericycle, which remind one in transverse section of those of the xylem-sheath in longitudinal section, are easily recognizable. The pericycle cells have the shape of sacs, while those of the xylem-sheath are tubular. The inner cortex is admirably preserved throughout its whole breadth up to its junction with the outer cortex. Its cells are thin-walled, but not so thin as those of the pericycle and sieve-tubes. The cells which surround the leaf-traces of the stele have black contents, which suggest that they were probably rich in starch. These layers of cells with black contents surrounding the leaf-traces and the stele are easily recognized, and give one the impression of a sheath. In other places the cells of the inner cortex do not contain any black substance and are lighter in tint. By this lighter colour they are distinguished from the darker and thicker-walled, roundish cells of the outer cortex which in longitudinal section appear to be prosenchymatous. The cells in the inner cortex in its middle portion are either isodiametric, or somewhat broader than long.

Leaf-traces.

The leaf-trace leaves the stele in the same manner as in a protostelic stem. The place of origin of a leaf-trace appears at the periphery of the stele as a prominence in the central part of which is one small group of protoxylem elements. At a somewhat higher level the base of this prominence becomes separated from the periphery of the xylem by a narrow-celled tissue of the xylem-sheath. At a still higher level the section of the leaf-trace, its cells filled with dark contents, is seen in the inner cortex as an oval strand in which the protoxylem has a mesarch position and is rather nearer to the adaxial side of the bundle (Pl. 32. fig. 4). The xylem is surrounded by a sheath of cells in which the elements of the second layer and sometimes of the third layer are characterized by brown contents. These cells are to be observed round the whole vascular bundle, but are especially well developed on the adaxial and abaxial sides. Immediately behind these cells, and generally separated from them by one or two layers of empty cells, occurs the phloem, readily recognized by the comparatively large sieve-tubes, which are usually arranged in the form of arcs three or four cells in width, both on the adaxial and abaxial sides of the bundle. In addition to the sieve-tubes, the phloem includes protophloem elements which occur on the outside as one or two layers of cells. Each bundle is surrounded by a series of cells with black contents which enclose it as a sheath uniting on the adaxial side of the bundle with a sheath of the same kind of cells with black contents that surrounds the stele. On the abaxial side of the bundle there may be about eight layers of such cells. This sheath is clearly limited on the outside by a layer of empty cells of the inner cortex, disposed sometimes with the longer axis at right-angles to the leaf-trace. The cells with black contents are described by Kidston and Gwynne-Vaughan in *Thamnopteris Schlechtendalii* as resistant cells, because as a rule only these cells are preserved round the leaf-trace of that species as it passes through the outer cortex. In *Thamnopteris Schlechtendalii* the resistant cells of the endodermis are clearly seen as a black line, bounding on the outside the cells of the pericycle which abut on the protophloem. But in *Thamnopteris Kidstoni*, in spite of the excellent preservation of the tissue, it is not possible to distinguish with certainty the endodermis and pericycle from the protophloem. This is especially difficult in the case of those leaf-traces where the phloem zone of the vascular bundle is feebly developed. Prosenchymatous cells appear on the adaxial side of the bundle; their number gradually increases until at a higher level they entirely replace the centripetal xylem; the oval mesarch vascular bundle becomes endarch, with a bay of parenchymatous tissue opposite the protoxylem which gives it a falcate form. On the adaxial side the cells of the xylem-sheath with their brown contents appear behind the empty parenchymatous cells of the bay, and at a higher level cells with black contents make their appearance; these cells represent the mucilaginous sacs which

occur in the pericycle of living *Osmundaceæ*. At this level and sometimes at a lower one may be seen the splitting of one protoxylem group into two. At a higher level the vascular bundle becomes more and more open on the adaxial side; at first it has a narrow falcate outline, and later assumes the form of a horseshoe (Pl. 32. fig. 5). The number of protoxylem groups is increased by the branching of the two original groups until in a leaf-trace on the point of passing from the inner cortex to the outer the number of protoxylem strands may be four or five. As a leaf-trace opens on the adaxial side the bay-like prominence of tissue surrounding it widens, and in this prominence it is possible to detect a band of phloem accompanied on the outside by a series of large cells with black contents (Pl. 32. fig. 6). Associated with the small-celled tissue of the pericycle are some parenchymatous cells of the inner cortex. The latter tissue may be accompanied by a thick-walled tissue having the features of the outer cortex. The large cells with black contents which make their appearance in the leaf-trace as it passes through the inner cortex occur as a group on its adaxial side. In the pericycle they appear to be characteristic of that tissue as it traverses the outer cortex, and especially when it passes through the petiole. In transverse section these cells appear to be vesicular, and in longitudinal section they resemble much elongated, septate fibres. Kidston and Gwynne-Vaughan call these cells mucilage sacs, and compare them with similar elements in the pericycle of living *Osmundaceæ*. They are undoubtedly mucilage sacs, and agree closely with those in the pericycle of recent *Osmundaceæ*. They are situated on both the adaxial and abaxial sides of the leaf-trace, along which the phloem forms an investment to the horseshoe-shaped bundle of the xylem immediately behind the protophloem. In the petiole the pericycle, which is feebly developed, as we have seen, in the leaf-trace during its passage from the inner cortex, becomes more developed and consists of five layers of small cells. The mucilage sacs are associated with these cells. On the abaxial side of the leaf-trace they are usually arranged in one or two series; on the adaxial side, where the pericycle zone attains a greater thickness, they are more irregularly arranged. On both the abaxial and adaxial side of the leaf-trace these arcs and mucilage sacs are enclosed by resistant cells which are stained brown, but agree closely with the black resistant cells which form the sheath of the leaf-trace in the inner cortex. As the fundamental tissue of the petiole is parenchymatous and light in colour, it is easily distinguished from the brown resistant cells surrounding the leaf-trace, and from the cells of the sclerenchyma which extend to the periphery and form in the petiole a border of characteristic outline. Outside this sclerenchymatous border is a narrow band of parenchyma which marks the limit of the petiole. This band represents the wings of the leaf stipules: the boundary between contiguous wings is indicated by a brown line. The wings of the stipules of

Thamnopteris Kidstoni are shorter and blunter than those of *Thamnopteris Schlechtendalii*, and, so far as one can see in the specimen, there is only one group of sclerenchyma in the form of a dot on each side of the stipule, and not two or three as in *Thamnopteris Schlechtendalii*. *Thamnopteris Kidstoni* is also characterized by the fact that the sides of the sclerenchymatous border in its outer portion are bent in the form of an arc curved outwards, while in *Thamnopteris Schlechtendalii* they are curved slightly inwards.

The Structure of the Roots.

The xylem bundles of the roots emerge from the periphery of the stele almost vertically, so that in this part of the transverse section of the stem they appear as if cut lengthwise. The bundle is diarch with obvious proto-xylem tracheæ. Usually the roots arise from the stele of the leaf-trace either singly or in pairs. Sometimes they are given off from the leaf-traces on the posterior and lateral parts of the xylem bundles as these bundles are becoming detached from the stele, or after they have been detached and lie in the inner cortex. The root bundles traverse the cortex of the stem in all possible directions, and in the transverse section of this region of the stem they appear either in longitudinal or transverse section. The transverse section reveals a diarch xylem bundle surrounded by a zone of thin-celled tissue sometimes filled with brown content. This zone contains about eight layers of cells which no doubt represent phloem; it is surrounded in its turn by a ring of four to five layers of empty cells which apparently represent the tissue of the inner cortex of the stem—orientated in relation to the root and forming its sheath. In longitudinal section the cells of the inner zone enclosing the vascular bundle of the root appear to be prosenchymatous; their walls are penetrated by irregularly distributed and rounded perforations varying in diameter and similar to the pits in the prosenchymatous cells of the outer cortex of the stem. The outer zone of light-coloured tissue in longitudinal section appears to consist of prosenchymatous cells with similar, irregularly distributed perforations in their walls—a fact that demonstrates that these perforations, wherever they occur, do not represent the structure of the wall but are due to a particular state of preservation. The vessels of the root, like those of the leaf-traces, are provided with multiseriate pits. As the root passes from the inner cortex to the outer part of the stem it is surrounded by its own cortex, the inner portion of which consists of thin-walled parenchyma and the outer part of sclerotic prosenchymatous cells. The roots as they traverse the parenchyma of the stipules of the petioles are provided with these two kinds of cortex and enclose in the centre a well-marked diarch vascular bundle surrounded by phloem which is not always well preserved.

THAMNOPTERIS GWYNNE-VAUGHANI *Zalesky*, n. sp. (Pl. 33. figs. 1-5.)

The transverse section of the stem of this fern, represented by a single specimen from the Permian deposits of the River Kozva in the basin of the Petchora River, has a central stele 11 mm. in diameter; the xylem reaches a diameter of about 9 mm., and consists of two distinct regions, an inner and an outer (Pl. 33. figs. 2 & 3). The inner xylem, about 7 mm. in diameter, occupies the central part of the vascular cylinder, and consists exclusively of short, wide xylem elements with reticulate pitting. There are no traces of parenchymatous tissues among the xylem elements present in the central part of the stele of *Thamnopteris Kidstoni*. The outer xylem, which encircles the inner, is composed of long and narrow tracheæ with multiseriate transversely elongated pits; its periphery is somewhat irregular in outline because of the prominences caused by the exit of leaf-traces which are given off at a wider angle than are those of *T. Kidstoni*. As a result of the course followed by the leaf-traces those next the stele in a transverse section of the stem are cut obliquely, and show multiseriate pits in the walls of the xylem elements. The angle at which the leaf-traces leave the stele varies from 22° to 30° . The xylem cylinder is surrounded by a sheath consisting of narrow and long cells. This sheath, which is badly preserved, includes three or four layers of cells, and is surrounded by another zone of four to six layers of cells made up of equally long but wider elements, in which it is not difficult to recognize the sieve-tubes of the phloem. This tissue is also badly preserved, and occurs only in some places on the circumference of the stele. The next zone of tissue has not been preserved, and beyond this is a single layer of badly preserved cells sometimes represented only by an irregular brown line representing the remains of the endodermis. The vacant space between this line and the phloem was occupied, one must suppose, by the pericycle, which is nowhere preserved. The endodermis was succeeded by the inner cortex, the tissue of which is only occasionally preserved. The cortical cells are parenchymatous and their diameter is much larger than that of the sieve-tubes. In the specimen examined the inner cortex occupies a zone about 9 mm. wide, and is clearly distinguished from the outer cortex (10 mm. broad) composed of thick-walled prosenchymatous elements. The leaf-traces passing through the inner and outer cortex enter the petioles which are at first in close contact, but nearer the periphery they are only slightly attached to one another. The petioles form a fairly thick covering to the stem.

The Departure of the Leaf-traces.

The leaf-traces leave the periphery of the stele at the places where prominences have been previously formed as a first step towards separation of the foliar bundles. As I have already pointed out, the sections of these

bundles near the stele are generally cut obliquely because of the wide angle at which they are given off. They bend sharply towards the periphery, and are seen as oval strands with an almost central protoxylem. At a higher level these bundles become somewhat elongated tangentially and, in consequence of this, they are cut more or less transversely in a transverse section of the stem (Pl. 33. fig. 4). The metaxylem group of small tracheids, which was previously almost central in its position, is shifted towards the adaxial side of the bundle and eventually passes from a mesarch to an endarch type of structure. At the same time the oval bundle becomes crescentic owing to curvature on the adaxial side. Examination of a transverse section of the stem shows that this change takes place very rapidly, and it is not possible to follow the gradual reduction in the centripetal xylem and its replacement by the parenchyma that has been observed also in the leaf-traces of *T. Kidstoni* and *T. Schlechtendalii*. This is explained by the sharp deviation of the leaf-trace from the stele and by the imperfect preservation of the tissues of the xylem-sheath and phloem which form round the vascular bundles a band composed of an imperfectly preserved mass of cells; this band abuts on a space left by the pericycle and is limited towards the outside by a brown line of endodermal cells. At a higher level the vascular bundles of the leaf-trace become more and more crescentic, and the single group of protoxylem branches into two (Pl. 33. fig. 5): one protoxylem group occurs at each end of the median line on the concave, adaxial half of the trace. Before the entrance of the leaf-trace into the outer cortex three of the protoxylem groups become differentiated; one group is situated on the median line and the other two on the flanks, one on each side. It is important to note that on the abaxial side of the vascular bundle at each horn of the crescentic xylem, which consists of tracheæ of the ordinary size, their occur along the edge linear groups of protoxylem. This occurrence of linear groups of narrow tracheæ on the flanks of the abaxial side of the bundle appears to be characteristic of *T. Gwynne-Vaughani*, as in *T. Kidstoni* and *T. Schlechtendalii* nothing similar has been observed. At its entrance into the outer cortex the leaf-trace is accompanied by an enveloping sheath of parenchymatous cells the tissue of which is badly preserved. Among the parenchymatous cells of this sheath, on the abaxial side of the trace and abutting on the phloem, there occur elements which correspond in structure and position to the secretory sacs that occupy a corresponding position in *T. Kidstoni*. The secretory sacs are accompanied by a group of cells with brown contents, and these cells appear to correspond to the elements in *T. Schlechtendalii* called by Kidston and Gwynne-Vaughan resistant cells. Similar cells are seen in certain leaf-traces on the abaxial side in the form of an arc which passes across to the adaxial side and envelops the whole leaf-trace. It is possible to observe also in certain leaf-traces secretory sacs on the abaxial side, where they occur as a narrow band immediately adjacent to

the phloem ; here, too, the cells have brown contents. In this part of its course the leaf-trace has a clearly marked horseshoe shape, and there are about six protoxylem groups on its inner face.

On the outer side of the leaf-trace there are no longer any of the tracheæ resembling protoxylem elements, which were present during its passage through the inner cortex. When the leaf-traces leave the outer cortex as they pass into the petioles, a portion of this cortex is seen behind them as a ring, and next to this ring is a parenchymatous tissue which belongs to the wings of the stipules and is pierced in many places by rootlets.

The Structure of the Roots.

The root arises either from the leaf-traces as they become apparent on the periphery of the stele, or after they have become detached from it ; in the latter case they can often be seen passing out in pairs on each side of the oval section of the leaf-trace, or one by one from its anterior surface. The root has a central vascular bundle of diarch structure which usually lies in a cavity left on the destruction of the phloem and inner cortex. This cavity is surrounded by the outer cortex and, nearer to the periphery, by a ring of sclerenchyma.

ZALESSKYA *Kilston & Gwynne-Vaughan.*

(Trans. R. Soc. Edinb. vol. xlv. 1908, p. 213.)

ZALESSKYA URALICA *Zalessky*, n. sp. (Pl. 34. figs. 1-3.)

We have only one transverse section of the stem of this species ; it was prepared from a specimen belonging to the artist Denisov-Oural'sky, and is from the Permian rocks of the Ural Mountains. Being unable to obtain a whole specimen I had to be satisfied with a single section which the owner kindly presented to me. The centre of the stem is occupied by a stele, slightly compressed along one diameter, which measures 10 mm. The other diameter is 12 mm. In the protostele is a space formed by the destruction of the central tissue of the stele, which undoubtedly occupied the whole space during the life of the plant. The stele consists of two kinds of xylem—an outer portion of long tracheæ of the usual width with multiseriate scalariform pits, and an inner portion composed of wider and shorter elements with irregularly distributed multiseriate and transversely elongated pits which give to the tracheæ a reticulate appearance. In the peripheral portion of the stele along its circumference, and at some distance from the edge, there are about 20 protoxylem groups of two or three elements each, which represent the mesarch protoxylems of the ends of the leaf-traces immersed in the stele. At a higher level these assume the form of prominences of the stele, each with a mesarch protoxylem : the prominences are eventually separated from the main part of the stele by the xylem-sheath and the phloem. The xylem is surrounded by a zone of elongated narrow

cells in four to five layers, and in this zone occur cells with brown contents; these are either scattered singly among the elements that have no brown contents or in groups. Next to this zone, serving as a xylem-sheath, is a band of wider phloem elements. These are sieve-tubes, and with them are sometimes seen small cells which represent phloem-parenchyma. The phloem is succeeded by a band of cells almost as large as the sieve-tubes, enclosing a brown mass. This band consists of five not quite regular layers. The inner series of these cells may be regarded as the pericycle, although the characteristic cells of the endodermis have not been found. The thickness of the inner cortex generally reaches 13 mm.; it is thus 7 mm. less than the thickness of the same tissue in *Zalesskya gracilis*. The outer cortex seen in my preparation, on a small extension of the circumference of the stem, is preserved only in its inner portion, and the thickness of this part does not exceed 6 mm. The leaf-traces, as seen in section near the stele, have an oval outline, and are separated from the cells of the inner cortex by a band of cells with brown contents. The protoxylem, even in leaf-traces that are very near the stele, occurs on the edge of the adaxial side so that the trace, which at its departure from the stele was mesarch, soon becomes endarch. The xylem-sheath of the vascular bundle and the phloem surrounding it are sometimes well enough preserved to show the sieve-tubes and, in the sheath, cells with brown contents. Nearer the periphery the leaf trace becomes reniform and the vascular bundle crescentic, first with one then with two protoxylem groups on its adaxial side. In the outer cortex the leaf-trace is surrounded by a sheath of parenchymatous cells of the inner cortex, and this is sickle-shaped. There are four protoxylem groups on its adaxial side.

The roots leave the periphery of the stele singly or in pairs. In the centre of the root is a diarch vascular bundle surrounded by phloem, beyond which is a thick cortex of parenchymatous cells stained a deep brown and sharply distinguished from the cells of the inner cortex of the stem through which the root passes. A few of the outer layers of the cortex are very deeply stained and have brown contents; it is possible that they are thick-walled cells. *Zalesskya uralica* is practically identical in structure with *Z. gracilis* and may be only a younger stem of that species. The difference consists in the smaller diameter of the stele, which is about 10 mm. broad, while *Z. gracilis* has a stele of 14 mm. and a narrower zone of inner cortex which reaches a breadth of 13 mm., while in *Z. gracilis* it is 20 mm. broad. The leaf-traces of *Z. uralica* are much smaller than those of *Z. gracilis* (Pl. 34, fig. 4). In view of the difficulty of deciding the question of relationship, it is more convenient to describe the Denisov-Ouralsky specimen under a separate name.

EXPLANATION OF THE PLATES.

PLATE 32.

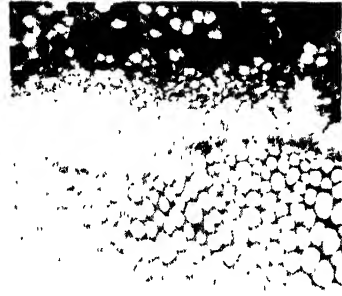
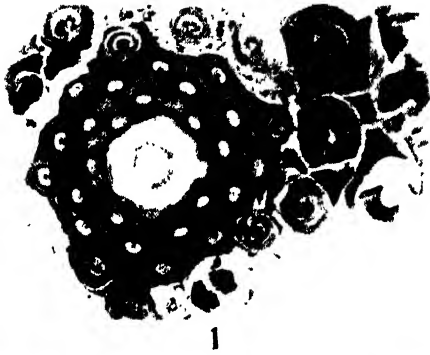
- Fig. 1. *Thamnopteris Kidstoni* Zalesky. Transverse section of the upper part of the specimen. $\times 2.4$.
- Fig. 2. *Thamnopteris Kidstoni* Zalesky. Part of a transverse section of the peripheral region of the stele and of the inner cortex. *o.xy.*, outer xylem ring; *xy.sh.*, xylem-sheath; *ph.*, phloem; *en.*, endodermis; *i.C.*, inner cortex. $\times 50$.
- Fig. 3. *Thamnopteris Kidstoni* Zalesky. Portion of a longitudinal section of the central and outer xylem of the stele. *c.xy.*, central xylem; *o.xy.*, outer xylem. $\times 50$.
- Fig. 4. *Thamnopteris Kidstoni* Zalesky. Transverse section of a leaf-trace in proximity to the stele. *X.*, outer xylem ring; *ph.*, phloem; *i.C.*, inner cortex. $\times 25.5$.
- Fig. 5. *Thamnopteris Kidstoni* Zalesky. Transverse section of a leaf-trace in the peripheral part of the inner cortex. $\times 25.5$.
- Fig. 6. *Thamnopteris Kidstoni* Zalesky. Transverse section of a leaf-trace in the sclerotic cortex. $\times 25.5$.

PLATE 33.

- Fig. 1. *Thamnopteris Gwynne-Vaughani* Zalesky. Transverse section. $\times 2.4$.
- Fig. 2. *Thamnopteris Gwynne-Vaughani* Zalesky. Part of a transverse section of the peripheral region of the stele. *o.xy.*, outer xylem ring; *ph.*, phloem. $\times 50$.
- Fig. 3. *Thamnopteris Gwynne-Vaughani* Zalesky. Part of a longitudinal section of the central and outer xylem of the stele. *c.xy.*, central xylem; *o.xy.*, outer xylem. $\times 50$.
- Fig. 4. *Thamnopteris Gwynne-Vaughani* Zalesky. Transverse section of a leaf-trace in proximity to the stele. *en.*, endodermis; *i.C.*, inner cortex. $\times 25.5$.
- Fig. 5. *Thamnopteris Gwynne-Vaughani* Zalesky. Transverse section of a leaf-trace in the peripheral part of the inner cortex. *s.C.*, sclerenchymatous cortex. $\times 25.5$.
- Fig. 6. *Bathypteris rhomboidea* Eichwald. Transverse section of a portion of the stele. *c.xy.*, central xylem; *o.xy.*, outer xylem ring. $\times 50$.
- Fig. 7. *Bathypteris rhomboidea* Eichwald. Transverse sections of leaf-traces in proximity to the stele. $\times 25.5$.

PLATE 34.

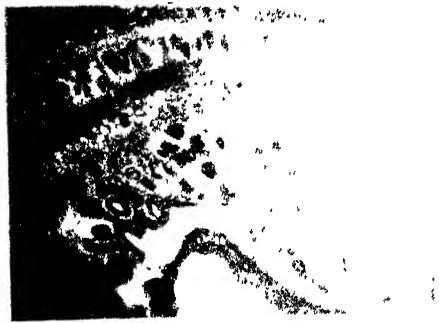
- Figs. 1-3. *Zalasskya uralica* Zalesky. Fig. 1, transverse section, nat. size. Fig. 2, transverse section of the peripheral part of the stele and the adjacent inner cortex. $\times 25.5$. Fig. 3, transverse section of the peripheral part of the stele. $\times 50$. *o.xy.*, outer xylem ring; *xy.sh.*, xylem-sheath; *ph.*, phloem.
- Figs. 4-5. *Zalasskya gracilis* Kidst. & Gwynne-Vaughan. Fig. 4, transverse section of peripheral part of the stele and adjacent part of the inner cortex. $\times 25.5$. Fig. 5, transverse section of the peripheral part of the stele. $\times 50$. *xy.*, outer xylem ring; *xy.sh.*, xylem-sheath; *ph.*, phloem.
- Figs. 6-7. *Thamnopteris Kidstoni* Zalesky. Portions of the central part of the stele in transverse and longitudinal section. $\times 27$. *c.xy.*, central xylem; *o.xy.*, inner part of the outer xylem ring; *p.c.*, the cells with brown contents are parenchymatous (the "primitive fibres" of C. E. Bertrand).



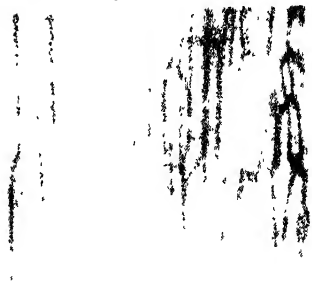
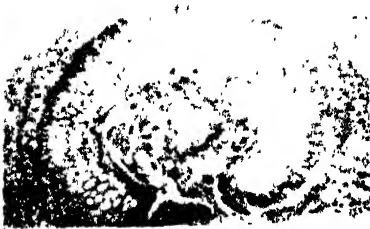
i.C.
en
ph
xy.sh.
o.xy

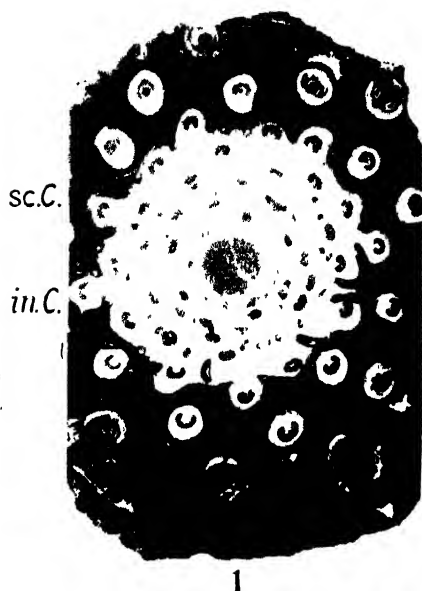


i.C.

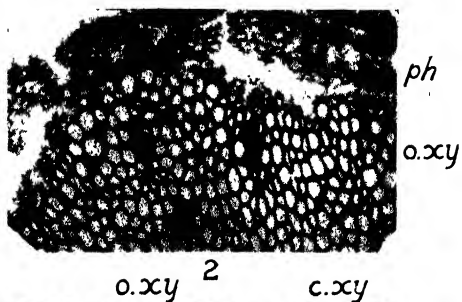


6
o.xy *c.xy*





1



3



6



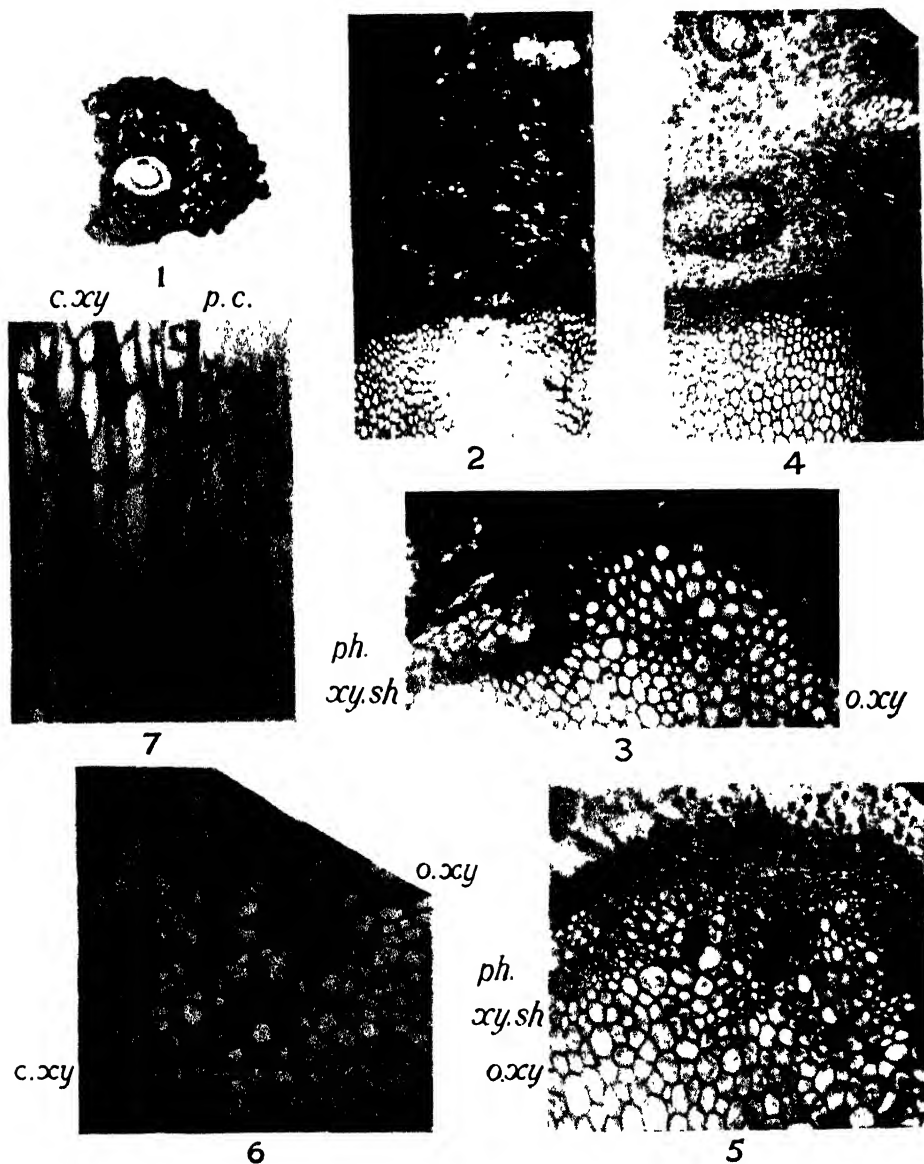
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NEW SPECIES OF PERMIAN OSMUNDACEÆ.

Notes on Indian Charophyta. By JAMES GROVES, F.L.S.

(PLATES 35, 36.)

[Read 3rd May, 1923.]

IN 1849 in a paper entitled "Characeæ Indiæ orientalis et insularum maris pacifici," published in Hooker's Journal of Botany, vol. i. pp. 292-301, Alexander Braun gave an account of the Charophyta then known to occur in India, enumerating eleven species. In 1873 he contributed a list of four species collected by S. Kurz in Burma to a paper by G. H. Zeller in the Journal of the Asiatic Society of Bengal, xlii. p. 193. The "Fragmente einer Monographie der Characeen," compiled by Dr. Nordstedt from Braun's MSS., and published in 1882, contained a number of additional Indian records.

Since the last-mentioned date many botanists have collected these plants in India, and the present paper is based on the examination of specimens which have passed through the hands of my late brother and myself in the interval, so far as we have been able to identify them.

In 1882 representatives of the two large genera *Chara* and *Nitella* only were known from India. Since that date *Nitellopsis*, *Lychnothamnus*, and *Tolypella* have been found, the last-named being represented by three species.

In the past, difficulty has been experienced in dealing with the specimens available, especially those of the *Nitelleæ*, so many of them being gathered at haphazard and imperfectly prepared. Of late years this is being largely remedied by the selection of healthy fruiting specimens, and still more by the preservation of portions in formalin. While even poor specimens of the *Characeæ* can by treatment usually be sufficiently restored for identification, I have not found this to be the case with the more delicate *Nitelleæ*. In dealing on this side with the more variable plants of the group, one is at a disadvantage in often having only a single specimen to examine, whereas on the spot an examination of a series might lead to a different conclusion. It is, therefore, in the hope that it may be of some little use in assisting and stimulating botanists working in India to the study of the group that the present paper has been written. Very much still remains to be worked out, especially in the direction of clearing up the limits and relations of the several species in some tangled groups. There are also probably other species to be found. Within the past two years, Mr. G. O. Allen has succeeded in adding three well-marked species to the list, collected within quite a small area.

I have included in the paper references to the species previously recorded so as to make it an enumeration of all those known to occur within the

Indian area, as laid down in C. B. Clarke's paper on the subsubareas of British India in the Society's Journal, xxxiv. p. 1, 1898; and I have made use of Mr. Clarke's districts in arranging the records.

I have added a rough key to the genera and species for the benefit of those to whom Braun and Nordstedt's invaluable "Fragmente" is not accessible. Like all keys, this must be used with caution or it may mislead in the case of extreme or abnormal forms. To the actual key characters I have added a few further particulars which may be of use.

Under each species indications of the known distribution outside the Indian area are given. Considering the many countries which have still been imperfectly searched for these plants, it is perhaps somewhat premature to attempt to generalize on their distribution, but the particulars furnished may afford some idea of the various elements which make up the Indian Charophyte-flora.

I have ventured to make a rather important modification of Braun's main divisions of the genus *Nitella*, by elevating to the first rank the sections *Homæoclemæ* and *Heteroclemæ* (*Homæophyllæ* and *Heterophyllæ*, Braun). The characters on which these are based appear to represent a more important and constant structural difference than the number of cells of which the ultimate ray is composed. Professor Ernst's paper "Die Stipularblätter von *Nitella hyalina* (DC.) Ag." (Viertelj. Naturf. Gesellsch. Zürich, xlix. 1904) has largely influenced me in coming to this conclusion.

My best thanks are due to the many friends and correspondents who have sent me specimens, to Sir David Prain for the opportunity of examining the entire collection of Charophyta at the Calcutta Botanic Gardens, and to the officials at Kew and in the Department of Botany of the British Museum, for referring specimens to us as well as for their kind assistance in consulting the herbaria. I am also much indebted to my friend Canon Bullock-Webster for his help in the examination of the oospore-membranes, to which difficult subject he has given special attention.

KEY TO THE GENERA.

- | | |
|--|------------------------|
| Coronula of oogonium composed of 10 cells in 2 tiers. Branchlets usually furcate. Stem and branchlets entirely without cortex | Nitellæ. |
| Antheridia terminal (in sp. 1 some also lateral), produced between the forks of the branchlets. Oogonia and oospores laterally compressed, hence elliptic in transverse section | 1. NITELLA. |
| Antheridia produced laterally at the nodes of the branchlets. Oogonia and oospores not laterally compressed, hence terete in transverse section | 2. TOLYPELLA. |
| Coronula of oogonium composed of 5 cells in 1 tier. Oogonia and antheridia produced laterally at the nodes of the branchlets. Oogonia and oospores not laterally compressed. Stem and branchlets corticate or ecorticate | Chares. |
| Stipulodes absent. Stem and branchlets ecorticate. Branchlets of 2-3 very long segments. Bract-cells 1-2 at a node, very long ... | 3. NITELLOPSIS. |

Stipulodes present, though sometimes rudimentary. Branchlets of 4 or more segments. Bract-cells normally 4 or more at a node.

Oogonia and antheridia produced side by side from separate peripheral cells of the branchlet node

4. *LYCHNOTHAMNUS*.

Oogonia and antheridia produced from the same peripheral cell of the branchlet-node, the antheridium below the oogonium

5. *CHARA*.

KEY TO THE SPECIES.

1. *NITELLA*.

Branchlets in each whorl in one series, nearly uniform in length and extent of furcation

Homœoclemae.

Dactyls (= ultimate rays) each consisting of a single cell

Anarthrodactylæ.

Dioecious. Oogonia clustered, conspicuously stalked: one antheridium sessile, terminal, others produced laterally at the same node, stalked. Branchlets once-forked, dactyls \pm mucronate. Coronula deciduous. Oospores c. 375–475 μ long.....

1. *N. mirabilis*.

Monœcious. Oogonia solitary, geminate, or rarely 3 together, sessile. Antheridia sessile, solitary. Branchlets once-forked, dactyls with very long acuminate points. Coronula persistent. Oospores c. 250–300 μ long

2. *N. acuminata*.

Dactyls each consisting of 2 or more cells.....

Arthrodactylæ.

Dactyls all or mostly 2-celled. Ultimate cell conical.

Dioecious.

Branchlets up to 4 times forked. Dactyls 3–5 unequal, primary rays elongated

3. *N. dispersa*.

Branchlets 2–3 times forked. Dactyls usually 6 equal, elongated cylindrical

4. *N. sp. nov.* ♀ ♂

Monœcious.

Dactyls not much abbreviated. Ultimate node usually fertile.

Rays at second forking usually 2–3. Primary ray less than half the length of the branchlet. Dactyls usually partially 3-celled, of unequal length, the lower cell rounded at apex, ultimate cell narrow mucro-like. Gametangia usually produced at all the forks of the branchlets

5. *N. mucronata*.

Rays at second forking 4–6, Dactyls uniformly 2-celled, of about equal length.

Gametangia usually produced at the first as well as other forks of the branchlets.

Plants of medium size, whorls attaining a diameter of at least 18 mm.

Young fruiting whorls not enveloped in a mucous cloud.

Primary rays elongated

6. *N. pseudo-flabellata*.

Young fruiting whorls enveloped in a mucous cloud.

Branchlets of nearly equal length, 2–3 times forked.

Penultimate ray not very short. Dactyls usually 5. Oospores c. 300 μ long. Mucous cloud very dense

7. *N. mucosa*.

Branchlets of very unequal length, 2–3 times forked.

Penultimate ray much abbreviated. Dactyls 5–6, very long and slender and curved at the base. Oospores c. 200–225 μ long. Mucous cloud inconspicuous

8. *N. Wattii*.

- Plants minute, diameter of whorls usually not exceeding 10 mm. Stem and branchlets extremely slender and flexuous. Branchlets usually 8 in a whorl, twice and occasionally 3 times forked. Dactyls very long and slender, lower cell tapering to the apex. Gametangia produced at the first and occasionally, at the second forking. Oospores 225–300 μ long, showing 6–8 broadly-flanged ridges 10. *N. bratrachosperma*.
- Gametangia not produced at first fork of the branchlets.
- Plant small, slender. Whorls distant, branchlets usually 6, short and rather rigid. Oospores c. 200–250 μ long, showing 7–8 low ridges. Membrane with conspicuous beaded large-meshed reticulation 9. *N. tenuissima*.
- Dactyls (at least some of them) very short and divergent, and arising from a sterile node.
- Coronula short, the upper cell not much longer than the lower.
- Oogonia solitary.
- Dactyls varying much in length, some not abbreviated and divergent. Oospores c. 250–400 μ long 11. *N. oligospora*.
- Dactyls extremely short, the lower cell often not much longer than broad. Oospores c. 200–220 μ long ... 12. *N. microglorhin*.
- Oogonia clustered. Dactyls mostly short and divergent.
- Oospores usually c. 250 μ long 13. *N. microcarpa*.
- Coronula elongate, some or all of the upper cells prolonged into a sharp point 14. *N. furcata*.
- Dactyls 2–3-celled, ultimate cell allantoid. Dioecious. Fruiting heads enveloped in a mucous cloud 15. *N. sp.* (*N. myrtri-tricha* prox.)
- Branchlets in each whorl in 3 series, those of the central series much longer and more compound than those of the upper and lower **Heteroclemæ.**
- Monœcious. Young fertile whorls enveloped in a mucous cloud 16. *N. hyalina*.

2. TOLYPELLA.

- Ultimate cells of branchlets conical **Conoideæ.**
- Stem stout. Sterile branchlets simple, much elongated. Oospore membrane very thin. Antheridia c. 300 μ in diameter 1. *T. prolifera*.
- Ultimate cells of branchlets allantoid **Allantoideæ.**
- Dioecious. [Oospores c. 250–300 μ long]. Antheridia c. 700 μ in diameter 2. *T. hispanica*.
- Monœcious. Oospores c. 300–375 μ long. Antheridia c. 325–375 μ in diameter 3. *T. glomerata*.

3. NITELLOPSIS.

- Dioecious. Plant very large. Branchlets \rightarrow 10 cm. long, of 2–3 segments; ultimate segment elongated. Oogonium c. 1200–1400 μ long, 1000–1200 μ thick; coronula small, *Nitella*-like. Antheridium c. 1000 μ in diameter. Producing large star-like bulbils 1. *N. obtusa*.

4. LYCHNOTHAMNUS.

- Monœcious. Stem imperfectly corticate. Stipulodes in a single circle, very long. Oogonium produced usually between two antheridia 1. *L. barbatus*.

5. *CHARA*.

- Stipulodes in a single circle** **Haplostephaneæ.**
Stem and branchlets entirely ecorticate.
Gametangia produced at the base of the whorl as well as at the branchlet-nodes. Stipulodes rudimentary.
Dioecious. Bract-cells moderately long. Oospores c. 500–550 μ long.
Antheridium c. 900 μ in diameter. Plant moderately stout 1. *C. Wallenhu.*
Monœcious. Bract-cells extremely short. Oospores c. 750–875 μ long. Antheridium c. 650 μ in diameter. Plant usually very stout 2. *C. corallina.*
Gametangia not produced at the base of the whorl. Stipulodes \pm developed, alternating with the branchlets. Oospores c. 525–650 μ long. Antheridium c. 275–325 μ in diam. Plant rather slender. 3. *C. Braunii.*
Stem corticate.
Branchlets ecorticate.
Oogonia and antheridia mostly produced at different branchlet-nodes. Branchlets 13–16 in a whorl, segments 6–8. Bract-cells numerous 4. *C. erythrogonia.*
Oogonia and antheridia produced at the same branchlet-nodes. Branchlets usually 10–12 in a whorl, segments about 5.
Ripe oospores golden-brown 5. *C. flaccida.*
Ripe oospores black 6. *C. gymnopitys.*
Branchlets \pm corticate, lowest segment ecorticate 7. *C. hydropitys.*
Stipulodes in a double circle **Diplostephaneæ.**
Rows of cortical-cells of the stem equalling the number of the branchlets **Haplostichæ.**
Dioecious. Spine-cells clustered. Cortical-cells of the branchlets equalling the number of the bract-cells 8. *C. canescens.*
Rows of cortical-cells of the stem twice as numerous as the branchlets. Cortical-cells of the branchlets twice as numerous as the bract-cells. **Diplostichæ.**
Secondary cortical-cells of the stem more prominent than the primary, so that the spine-cells appear to lie in furrows **Aulacanthæ.**
Branchlet-segments mostly corticate. Gametangia not produced above ecorticate segments. Spine-cells solitary. Ripe oospores normally brown, very rarely black 9. *C. vulgaris.*
Branchlet-segments wholly or partially ecorticate. Some gametangia produced above ecorticate segments. Spine-cells solitary. Ripe oospores brown 10. *C. gymnophylla.*
Primary cortical-cells of the stem more prominent than the secondary, so that the spine-cells appear to stand on ridges **Tylacanthæ.**
Oospores black. Stipulodes usually somewhat irregular 11. *C. contraria.*
Rows of cortical-cells of the stem three times as numerous as the branchlets **Triplostichæ.**
Lowest branchlet-segment corticate.
Dioecious. Stipulodes \pm elongated. Spine-cells rudimentary 12. *C. infirma.*
Monœcious.
Lowest branchlet-segment moderately long. Cortical-cells of the branchlets twice as numerous as the bract-cells. Stipulodes and spine-cells rudimentary 13. *C. fragilis.*
Lowest branchlet-segment very short. Cortical-cells of the branchlets about three times as numerous as the bract-cells. Stipulodes elongated acute. Spine-cells minute acute 14. *C. brachypus.*
Lowest branchlet-segment ecorticate. Cortical-cells of the branchlets three times as numerous as the bract-cells. Stipulodes elongated acute. Spine-cells acute. Monœcious 15. *C. zeylanica.*

1. NITELLA Agardh.

I. Homœoclemæ.

i. Anarthrodactylæ.

1. N. MIRABILIS Nordstedt, species nova. (Pl. 35.)

Homœoclema anarthrodactyla semel furcata (glœocephala?) diœcia. Oogonia et antheridia utræque aggregata plerumque longipedicellatæ; dactyli \pm mucronati.

Diœcious. Stem rather slender, diam. c. 500 μ . Whorls of 6-8 long branchlets. Branchlets once-furcate, the primary rays averaging about $\frac{2}{3}$ the length of the entire branchlet; dactyls 2-4, usually 3, long, slender (diam. c. 125 μ), equal, divergent, terminating in \pm mucronate points. Oogonia usually clustered 2-3 together, a few solitary, conspicuously stalked, c. 550-700 μ long (excl. cor.), 475-575 μ broad; spiral cells swelling slightly at their apex, usually showing 8 convolutions; coronula broadly conical, c. 50 μ high, 75 μ broad, deciduous. Oospores c. 375-475 μ long, 325-375 μ broad, c. 300 μ thick, deep golden-brown, showing 6 thin broadly-flanged ridges; membrane finely granulate. Antheridia clustered 2-3 together, central (when present) sessile, the lateral stalked, diameter c. 500-600 μ .

In some shallow pools in the bed of an ancient river, Gonda, Oudh (Dist. 6). 14 Jan. 1922, no. 1; Dec. 1923, nos. 21, 23. *G. Q. Allen*.

This remarkable species was first discriminated by Dr. Nordstedt, who gave it the ms. name *N. mirabilis*, from specimens collected in Yunnan, China, 29 April, 1908, by Fr. Ducloux (no. 5856), which are preserved in the national herbarium in Paris. Dr. Nordstedt kindly afforded my late brother and myself the opportunity of examining the specimens, and has asked me to describe the plant.

Mr. Allen's discovery of it in India is of great interest, and his carefully selected and admirably prepared specimens have supplied the means of describing the habit of the plant and of figuring it, the original Chinese specimens being poor. The Indian specimens show a rather small plant, about 15-20 cm. in height, with long branchlets, and a generally lax habit resembling that of the European *N. syncarpa*, the male plant forming small dense heads. The stem and branchlets show well-marked annular incrustation. The Chinese plant has rather larger oogonia and oospores than that from India. The very young fertile heads of both plants appear to be enveloped in a slight mucous cloud.

The outstanding features of the species are the clustered long-stalked oogonia and the antheridia in clusters of 2-3, some with conspicuously long stalks, originating laterally in the same manner as the dactyls, one being usually sessile in its normal position. The stalks of the oogonia are sometimes extremely long; I have measured one of about 5 mm.

2. *NITELLA ACUMINATA* Braun.

1. Below Simla (4000'), 1885. *Sir G. Watt.*
5. Bogoda, Hasaribagh, Chota Nagpur, 1873, no. 20712; Purulia, Chota Nagpur, 1874, no. 25259. *C. R. Clarke.*
6. Forbesganj, Dist. Purneah, 1906, no. 27327. *I. H. Burkill.*
Gonda, Oudh, 1922, no. 4. *G. O. Allen.*
11. Penang, 1896, no. 52. *T. B. Blow.*
Kuala Lumpur, F.M.S., 1922, no. 764. *H. P. Hacker.* A form with very short dactyls.
- 11*. Singapore, 1896, no. 51. *T. B. Blow.*
Sauglin, Singapore, 1898, no. 9137. *H. N. Ridley.*

Recorded by Braun from (3) Concan, and (5) Coromandel Coast.

N. acuminata is a widely distributed tropical and sub-tropical species, occurring also in Ceylon, the East Indian Archipelago, and the Philippine I. : Mauritius and Madagascar; North America, reaching as far north as New York State; West Indies; South America.

ii. *Arthrodactylæ.*3. *N. DISPERSA* Braun.

Recorded by Braun from (3) Concan and (8) Assam.

4. *N. sp. nova?*

Homæoclema arthrodactyla (semper bicellulata) flabellata glæocephala dicecia.

9. Yawnglwe River, near head of Inle Valley, Southern Shan States, 10th March, 1922, no. 3. *N. Annandale.*

Dr. Annandale's specimen consists of the male plant only, and I have not thought it desirable therefore to give it a name as in the absence of the female plant it is not possible to draw up a satisfactory description, or to compare it with the allied Australian species. It is a striking plant with fertile whorls about 20 mm. in diameter invested in a dense mucilaginous cloud. The stem is about 750 μ in diameter, the branchlets usually 8, twice or three times forked, with about 8 rays at the first forking; the penultimate rays are not much shorter than the dactyls which are about 6 in number, elongated, of about equal length, the lower cell slightly narrowing at the apex, the apical cell very narrow and acute. The antheridia, about 450 μ in diameter, are produced at all the nodes, though less frequently at the first node.

It is much to be hoped that the plant may be again collected, so that female examples may be obtained.

5. *NITELLA MUCRONATA* Miquel, *sens. lat.*3. Chiplun, 1914. *S. P. Agharkar.*6. Benares. *B. Sahni.*Gonda, Oudh, 1922, nos. 5, 8, 11, 16. *G. O. Allen.*9. Nong Shong Khong, Manipur, 3900', 1882, nos. 6306-7; Lareain, Manipur, 1882, no. 6296 (part); Kittiemala, Manipur, 1882, no. 6820 (part)? *Sir G. Watt.*Katha, 1904, no. 22666; Kawkaveik, 1904, no. 24474. *I. H. Burkill.*

The above represent a series of slightly different forms which, from the material at present available, I can only refer to *N. mucronata* in a broad sense. The doubtful plant from Manipur under no. 6820 shows a resemblance to *N. oligospira*, but some of the ultimate rays are 3-celled and few are much abbreviated. There is a considerable difference between the decoration of the oospore-membranes of the several plants here included under *N. mucronata*, some having the well-marked regular reticulation of the European plant, while in others the protuberant portions are only imperfectly connected.

N. mucronata, including its subspecies, is widely distributed, occurring in most parts of Europe and in Asia, Africa, and North America.

6. *N. PSEUDO-FLABELLATA* Braun.

Recorded by Braun from (8) Chittagong, and from Java, Borneo, and China.

Further investigation is necessary as regards this rather ambiguous species. In the "Fragmente" from which the name must date *N. pseudo-flabellata*, with the exception of forma *mucosa* Nordst., is treated as gymnocephalous, but, in order to be sure of this character, the plant must be observed in its early stages, as later on in some at least of the glæocephalous species the mucous cloud is not apparent. This fact has probably led to some confusion. Dr. Allen regarded the elongated primary ray as an important character, but included the glæocephalous plants, here separated as *N. mucosa*. The larger number of rays especially at the second and ultimate furcations and the greater number and approximately equal length of the uniformly 2-celled dactyls seem to distinguish it from *N. mucronata*.

7. *N. MUCOSA* J. Groves. *N. pseudo-flabellata* f. *mucosa* Nordst.10 or 11. Galang, Malay Peninsula, 1899, no. 10827. *H. N. Ridley.*11*. Cluny Lake, Singapore, 1920. *T. F. Chipp*; 1923, no. 10016. *R. E. Holttum.*

An immature plant collected by Sir G. Watt in 1885 below Simla at 4000' probably also belongs to this species.

N. mucosa was originally described as f. *mucosa* from New Zealand; plants apparently referable to it have been collected in Ceylon, Japan, and Tonkin.

8. *NITELLA WATTII* species nova. (Pl. 36.)

Homœoclema arthrodactyla flabellata macrodactyla glæcephala monoica. Ramuli inæquales plerumque tris-furcati, partim aliquando quaterfurcati. Radius primarius elongatus, dimidium ramuli totæ longitudinis superans; radii penultimi multo abbreviati, dactylos 5-6 elongatos, semper bicellulatos gerentes.

Stem slender (diam. c. $400\ \mu$). Whorls of 6-7 rather short branchlets of unequal length. Branchlets usually three times furcate, some of the quaternary rays occasionally again divided. Primary ray exceeding half the length of the entire branchlet; secondary rays 6-7 usually elongated; tertiary rays 5-6, some simple, some forked, the latter usually very short; dactyls 5-6, very slender (diam. c. $40-65\ \mu$), when quaternary or quinary more than twice, often three times, as long as the penultimate rays, always 2-celled, the lower cell much curved at the base, slightly tapering at the apex, ultimate cell elongate-conical, c. $50-80\ \mu$ long, $20-25\ \mu$ broad, with long acuminate point.

Oogonia solitary, produced at the third (and fourth when present), and occasionally at the second, node, c. $300-320\ \mu$ long (excl. coronula), $225-240\ \mu$ broad, spiral-cells showing 8-10 convolutions; coronula c. $30\ \mu$ high, $45\ \mu$ broad. Oospores broadly ellipsoid, c. $200-225\ \mu$ long, $175-200\ \mu$ broad, $125\ \mu$ thick, showing 7-8 thin fairly prominent ridges with narrow flanges, scarcely crested, warm chestnut-brown; membrane with vermiform decoration. Antheridia produced usually at the second, sometimes at the first node, diameter c. $225\ \mu$.

6. Mugra (prior to 1882), no. 306. *Sir G. Watt*.

Sir George Watt's larger specimen shows a plant about 20 cm. high, of slender graceful habit, the fruiting whorls not forming distinct heads. The mucous cloud is hardly perceptible to the naked eye in the dried plant. The outstanding features seem to be the unequal length of the branchlets in the same whorl, and the much abbreviated penultimate rays, surmounted by the cluster of dactyls, presenting a tassel-like appearance.

9. *N. TENUISSIMA* Kütz.

A form of this species, var. *byssoides*, is recorded by Braun from (5) the coast of (6)romandel (*Billanger* 1826-8). I have not seen a specimen. It is to be hoped that it may be again collected, as from Braun's remarks it would appear to differ considerably from the typical form.

N. tenuissima occurs in many countries in Europe, in N. Africa, N. America, and the West Indies.

10. *N. BATRACHOSPERMA* Braun.

6. Gonda, Oudh, 30th Dec. 1922, no. 24. *G. O. Allen*.

The first record for India for this minute species. A doubtful plant

collected by Professor Agharkar in 1912, in Kathiawar, agrees with *N. batrachosperma* in having the branchlets usually only twice forked, with gametangia produced at the first forking, but has 6 branchlets in a whorl, and lacks the characteristic broad flanges of the oospore ridges.

The distribution of the species as at present known is very disconnected, but it is probably often overlooked on account of its diminutive size. It has been found in a number of European countries, in Japan, North America, and Australia.

11. NITELLA OLIGOSPIRA Braun.

6. Bengal. *Griffith (Herb. Calcutta).*

Sueksagur, near Calcutta, no. 303. *Sir G. Watt.*

Recorded by Braun from (2) Lahore and (10) Pegu, also so named by him from Nowkream, Khasia, 5000', *Herb. Hooker*, and from Nicobar I. by Nordstedt.

N. oligospira is characteristically a tropical species, occurring in Ceylon, Java, Japan; Comoro Islands; Texas; West Indies; Venezuela and Brazil.

12. N. MICROGLOCHIN Braun.

A specimen collected by G. M. Woodrow at Ratnagiri, 1893, no. 2, has the remarkably short dactyls of this species, but I have not seen ripe fruit.

N. microglochin was described by Braun from a plant collected by S. Kurz in the Kolodyne Valley, Aracan, and I do not know of any other record of it. It may possibly be merely an extreme form of one of the other species of the *Brachydactyle*.

13. N. MICROCARPA Braun.

11. Gunong Tungul Dindings, Perak, 1896, no. 7142; Bruar Dindings, Perak, 1896, no. 7144. *H. N. Ridley.*

Penang, no. 1887. *H. N. Ridley.*

Occurs also in Ceylon and Java; South Africa and Madagascar; North and South America, and West Indies.

14. N. FURCATA Agardh (1824). *Chara furcata* Bruzel. (1824), Roxburgh (1832); *N. Roxburghii* Braun (1849), not *C. Roxburghii* Braun (1835).

11*. Singapore, 1896. *T. B. Blow.*

Recorded by Braun from (5) Coromandel Coast, (10) Pegu, and the Nicobar Islands. Roxburgh recorded it from (6) "tanks and stagnant sweet water near Calcutta." Although there seems to have been some confusion as to the earlier plants circulated under this name, I think there can be none as regards the identification of Roxburgh's plant, and therefore that of Agardh and Bruzelius based thereon. Both the latter authors say "nuculis

alaribus, aggregatis." Roxburgh's drawing of the plant at Kew shows the remarkable character of the coronula and his description in 'Flora Indica,' iii. p. 564, could hardly belong to any other species.

The distribution of *N. furcata* seems to be a restricted one. It is at present known from India, Ceylon, Malay Archipelago, and Philippine Islands, but *N. japonica* Allen, from Japan, and *N. guineensis* Kütz., from W. Africa, are apparently nearly related thereto.

15. *NITELLA* sp. *N. MYRIOTRICHA* Kütz. *prox.*

3. Amboli, Western Ghats, 1902, no. 17073. *I. H. Burkill.*

8. Tsillong, Khasia, 1867, no. 3762. *C. B. Clarke.*

Both these plants belong to Braun's section *Polyarthrodactylon* and agree in the main with the Australian *N. myriotricha*, having 2-3-celled dactyls with allantoid-mucronate apical cells, being dioecious, and having the female plant forming small fruiting heads enveloped in mucus. There are, however, some minor points of difference between the Australian plant and those from India, as well as between the Indian plants themselves. Further specimens of both the latter are desirable in order to arrive at a satisfactory determination.

II. *Heteroclemæ.*

16. *N. HYALINA* Agardh.

2. Gwalior, 1890. *C. Muries.*

Depalpur, Indore State, 1914. *S. P. Agharkar.*

Watrak River, 1915, no. 1192. *L. J. Sedgwick.*

3. Moota River, Poona, 1895. *G. M. Woodrow.*

Kattiawar. *Sir G. Watt.*

Chiplun Dist., Ratnagiri, 1913. *S. P. Agharkar.*

5. Saugor. *Jerdon.*

Chanda Dist., 1889, no. 10051 (part). *J. F. Duthie.*

Betwa River, Bundelkund, and near Rājghat, 1888, nos. 7091-2 (part). *J. F. Duthie.*

6. Botanic Garden, Shibpur, Calcutta, 1901. *Sir D. Prain.*

Benares, 1908. *T. B. Blou.*

Gonda, Oudh, 1921-2, nos. 10, 19. *G. O. Allen.*

10. Tataungtoea (?), south of Prome, Lower Burma, 1904, no. 23843. *I. H. Burkill.*

Recorded by Braun from (2) Baluchistan, (3) Nilgiri Hills, and (6) Prov. Behar.

N. hyalina is a very widely distributed species occurring over a large part of Europe : Soongaria, Persia, China, Japan ; N. and S. Africa ; N. and S. America, West Indies ; Australia, New Zealand, and New Caledonia.

2. TOLYPELLA Leonhardi.

I. Conoideæ.

1. T. PROLIFERA Leonh.

6. Gonda, Oudh, Dec. 1922, nos. 22, 25, 29. *G. O. Allen.*

Not, I believe, hitherto recorded from any part of Asia, but an immature specimen collected by J. M. Delavay in 1887 in Yunnan, China, almost certainly belongs to this species.

T. prolifera occurs in a few scattered localities in Europe and North America.

II. Allantoideæ.

2. T. HISPANICA Nordst.

2. Quetta, 7th April, 1888, no. 8747. *J. F. Duthie.* The male plant only.

T. hispanica occurs in several localities on the Northern and Southern shores of the Mediterranean and in Persia.

3. T. GLOMERATA Leonh.

1. Sumbal, Kashmir, at 5200', 1896, no. 129. *Col. H. H. Johnston.*

2. Quetta, 13th April, 1888, no. 3562. *J. H. Luce.*

Mr. Arthur Bennett kindly gave us a small portion of a plant collected by Potanin in Western Kansu, China, which probably belongs to this species, but the specimen is hardly sufficient for identification. It is recorded from Ispahan, Persia, 1868, by C. Haussknecht, but the specimens of Haussknecht's from that place which I have examined belong to *T. hispanica*. Braun ("Fragmente," p. 96) refers to a doubtful plant from "*aquis pigris deserte Cumani*" as being either *T. nidifica* or a variety of the present species.

T. glomerata is widely distributed in Europe. It occurs also in N. and S. Africa, N. America, and Tasmania.

3. NITELLOPSIS Hy.

1. N. OBTUSA J. Groves. *Lychnothamnus stelliger* Braun.

1. Dhal Lake, near Srinagar, Kashmir, Sept., Oct. 1921. *G. O. Allen.*
♀ and ♂.

9. Fort Stedman, Upper Burma, 1892. *Abdul Huk.* Sterile.

We had little doubt as to the identity of the Fort Stedman plant, but, in the absence of gametangia, and in view of the great distance from any known locality for the species, hesitated to record it. Mr. Allen's recent discovery of it in Kashmir removes the element of doubt as to the Burmese plant.

With the exception of these localities *N. obtusa* is not known to occur outside Europe, where it is an uncommon plant, though widely distributed.

4. LYCHNOTHAMNUS Leonh.

1. *L. BARBATUS* Leonh.1. Dhal Lake, near Srinagar, Kashmir, Oct., Sept. 1921. *G. O. Allen.*2. Depalpur, Indore State, March 1914. *S. P. Agharkar.*6. Bengal, prior to 1882, nos. 308 & 315. *Sir G. Watt.*Gonda, Oudh, 15th Dec. 1921 ; 1922, nos. 2, 15, 20, 27, 28 ; 1923, no. 32. *G. O. Allen.*

Prior to Sir G. Watt's discovery of this remarkably distinct plant in India, its known distribution was confined to a small part of Europe, viz. :—Germany, Italy, and a single locality in Eastern France.

5. CHARA Linn.

1. *Haplostephane*.1. *C. WALLICHII* Braun.6. Gonda, Oudh (♀ and ♂), 15th Oct., Nov. (no. 9), Dec. (no. 26), 1922 ; Lucknow, 8th Jan. 1923, no. 30. *G. O. Allen.*

Mr. Allen's rediscovery of this species is an important one. The specimen in the Wallich herbarium, collected in 1809 at Pirgunj (6), from which the species was described, consisted of the male plant only, and it had not, I believe, since been collected. Mr. Allen's specimens of the female plant enable me to add particulars of the fruit. The vegetative parts of the female plant correspond fairly closely with Braun's description of the male. The oogonia are clustered at the base of the whorl, both in- and outside the branchlets, and at the first and second branchlet-nodes, usually 2-3 together at the former and 1 at the latter, and are much exceeded in length by the adjacent bract-cells. They are broadly ellipsoid, about $850-875\mu$ long, $550-575\mu$ broad, the spiral-cells showing 7-8 convolutions ; the coronula nearly straight, about 250μ broad, 150μ high. The oospores are broadly-ellipsoid to ellipsoid-cylindrical, \pm truncate at both ends, especially at the base, about $500-550\mu$ long, $375-450\mu$ broad (excl. ridges), showing 6-7 strong prominent ridges, with very short claws ; membrane thick, firm and opaque.

Closely allied to the Australasian *C. australis* (also dioecious) and to *C. corallina* (monoecious), but differing from both in the smaller fruits, elongated apical segments of the branchlets, and the well-developed bract-cells. From *C. Braunii* it differs in producing gametangia at the base of the whorl as well as at the branchlet-nodes.

2. *C. CORALLINA* Willd.2. Depalpur, Indore State, 1914. *S. P. Agharkar.*3. Malabar, no. 138. *Herb. Kew.* Chiplun, Ratnagiri, 1914. *S. P. Agharkar.*

6. Calcutta, 1864, no. 1924. *S. Kurz.*
Howrah, no. 2593; Mugra; Sucksagur, no. 2594. *Sir G. Watt.*
Benares, 1919. *B. Sahni* (comm. *C. V. B. Marquand*).
Gonda, Oudh, 1921; 1922, nos. 13, 18. *G. O. Allen.*
10. Kyantaw, Dist. Akyab, 1907, no. 28275. *I. H. Burkill.*
- 10*. S. Andaman I., 1890. *Sir G. King.*

Recorded by Braun from (5) Tranquebar and Madras, and (6?) Bengal.
Occurs also in Ceylon and the Philippine Islands.

3. CHARA BRAUNII Gmel.

1. Dulash Kula, 6000', 1888, nos. 9660-1. *Sir G. Watt.*
6. Gonda, Oudh, 1921. *G. O. Allen.*
8. Assam, 1882. *Simons.*
9. Nong Shong Khong, Manipur, 1882, no. 6305; Lareain, 1882-4, no. 6296. *Sir G. Watt.*

Recorded by Braun from (1) Naini Tal, Kumaon; (5) Gengu, Coromandel; (6) Behar, Bengal.

C. Braunii is widely distributed, occurring in many parts of Asia (Siberia, Syria, Java, Tonquin, China, Japan, Philippine I.); over a large part of Europe, in N. and S. Africa, N. and S. America, Australia, New Zealand, and Sandwich I.

4. C. BRYTHROGYNA Griffith. *C. Griffithii* Braun.

6. Between Kissongunga and Sitalya, 1868, no. 1884. *S. Kurz.*
Chitowni, near Nepal frontier, Dharbanga Dist., 1907, no. 29320.
I. H. Burkill.

Described by Griffith from Serampore, and recorded by Braun from Saharanpore Botanic Garden; also found in Cochin China and Java.

Braun's action in setting aside the name published by Griffith, with a very fair description, in favour of a MS. name of his own, seems indefensible.

5. C. FLACCIDA Braun.

- 3, or 5. Bhainsi, Nizam's Dom., 1905. *I. H. Burkill.*
11. I. of Langkari. *C. Curtis.*

Bottom of Lake Dayong Bonting, 1890, Fl. of Kedah no. 2587.
C. Curtis. A form with unusually short stipulodes.

Recorded by Braun from (5) Madras and (6?) Lower Bengal. The golden-brown ripe oospores afford the only character that I know of to distinguish this from the next species, and in many specimens which have passed through our hands the fruits were immature. It is therefore probably much more widely distributed in India than the above localities imply.

Outside India *C. flaccida* has been collected in the Libyan Desert, Ceylon, Tonkin, Borneo, Celebes, and the Philippine and Marianne Islands.

6. *CHARA GYMNOPIITYS* Braun.

2. Depalpur, Indore State, 1914. *S. P. Agharkar*.
 11. Kuala Lumpur, Fed. Malay States, 1922, nos. 705 *b* & 710. *H. P. Hacker*.
 11*. Singapore Gardens Lake, 1896. *T. B. Blow* & (nos. 6915 & 9137) *H. N. Ridley*.

Recorded by Braun from (10) Kolodyne Valley, Aracan. Some of the plants referred to as unidentified under the foregoing, no doubt belong to this species.

Braun separated his *C. Benthami* from *C. gymnopitys* by the comparative number of stipulodes and branchlets, the former having the same number of each, the latter double as many stipulodes as branchlets, this character throwing them into different sub-sections of the *Haplostephaneæ*. In his notes included in the "Fragmente," p. 118, he recognizes that this is unsatisfactory, the character being inconstant. It frequently happens that there are more stipulodes than branchlets, yet not double the number, and we have not been able to separate the specimens we have examined satisfactorily by this character. As far as I can at present see, I can only regard *C. Benthami* at most as a variety of *C. gymnopitys*. The specimens from Kuala Lumpur and Singapore would come under *C. Benthami*. In the whorls of the Depalpur plant which I have examined the stipulodes are rather more numerous.

C. gymnopitys is widely distributed, occurring in Socotra, China, Japan, Philippine Islands; Cape Colony; N. America (New York and Michigan); Australia, Tasmania, New Zealand, and New Caledonia.

7. *C. HYDROPIITYS* * Reichb.

6. Gonda, Oudh, 1922, no. 3. *G. O. Allen*.

C. hydropitys occurs also in Ceylon; N. Africa; and N. and S. America, the range being within 30° north and south of the Equator, except in N. America, where it runs up to just over 40° in the Eastern United States.

II. *Diplostephaneæ*.i. *Haplostichæ*.8. *C. CANESCENS* Loisel. *C. crinita* Wallr.

2. Quetta, Baluchistan, 1888, no. 3837. *J. H. Lace*, Hb. *Watt*.

Recorded by Braun from (2) Baluchistan and Peshawar.

C. canescens occurs in Afghanistan, Siberia, and China. It is known from a great part of Europe, N. Africa (Gran Canaria and Egypt), and the N.E. United States.

* Spelt *hydropithys* by Reichenbach.

ii. *Diplostichæ*.* *Aulacanthæ*.9. *CHARA VULGARIS* L. *C. fistida* Braun.

This polymorphic species is very widely distributed in India proper. We have seen specimens from districts 1, 2, 3, 5, 6, and 7, also from 9, Manipur. A form collected by Mrs. Tristram from (2) near Campbellpur has unusually large antheridia (diam. $\rightarrow 525 \mu$).

A world-wide species.

10. *C. GYMNOPHYLLA* Braun.

9. Inn Gaung, c. 3800', nos. 1-2; middle of Inle Valley, c. 3000', no. 4; N. of Fort Stedman, Inle Valley, c. 3000', no. 5; Taunggyi, 4700', no. 7; Loi-An near Kalaw, no. 8; all in the Southern Shan States, 1922. *N. Annandale*.

Closely allied to and much resembling *C. vulgaris* and perhaps best regarded as a subspecies thereof, distinguished by its \pm ecorticate branchlets, gametangia being produced at nodes not giving rise to a cortex.

C. gymnophylla is characteristically a Mediterranean species occurring all along the south of Europe, in Syria, and in several parts of N. and S. Africa, also in the Caucasus, and it is known from one locality in China.

** *Tylacanthæ*.11. *C. CONTRARIA* Kütz.

Widely distributed in India proper, occurring in many localities in districts 1, 2, 3, 6, and 7, also in 9, Northern Shan States.

C. contraria is a wide-spread species occurring almost throughout Europe, in some other parts of Asia, in North and South Africa, in North and South America, and in Australasia.

iii. *Triplostichæ*.* *Phlæopodes*.12. *C. INFIRMA* Braun.

This rather doubtful species was described from specimens collected by Griffith in Afghanistan (without further indication of locality), numbered 4, 112, & 128. The principal characters relied upon to separate it from the other dioecious species of the section were the strongly-developed stipulodes coupled with rudimentary spine-cells. Specimens from the two localities mentioned below, however, seem to belong to this species, although the stipulodes are by no means always well-developed, and the bracts and bracteoles are smaller than in Griffith's plant. The cortex is similar, the

spine-cells are always rudimentary, and the antheridium is of the same diameter. Unfortunately the fruit in Col. Johnston's plant is too young for comparison.

1. Kurparthal, near Naini Tal, Kumaon, 5000-6000', 1885, no. 5228. *J. F. Duthie*. ♂.

2. Near Peshawar, Punjab, 1000', 1895-7. *Col. H. H. Johnston*. ♀ ♂.

An immature ♀ plant from Baltisthan, Skardo, Kashmir (1), 1876, no. 30503, *C. B. Clarke*, may also belong to this species.

13. CHARA FRAGILIS Desv.

1. Dhal Lake, Kashmir, 1921. *G. O. Allen*.

2. Gwalior. *Maries*. Bhim, Merwara, Khandwa Dist., 1886, no. 5257. *J. F. Duthie*.

3. Bombay. *Major Hobson*. River at Poona, 1895. *G. M. Woodrow*
3? Pools in bed of Nerbudda, Khandwa Dist., 1889, no. 8549 (part). *J. F. Duthie*.

6. Patna, 1812. *Hb. Wallich*. Sucksagur, prior to 1882. *Sir G. Watt*.
Gonda, Oudh, 1922, nos. 12, 17. *G. O. Allen*.

A world-wide species.

14. C. BRACHYPUS Braun.

2. Depalpur, Indore State, 1914. *S. P. Agharkar*.

3. W. Khandesh, 1899, no. 33217. *I. H. Burkill*.

Beyt, Dwarka, Kathiawar, 1912; Chiplun Dist., Ratnagiri, 1913
S. P. Agharkar.

5. Chanda Dist., Central Prov., 1889, no. 10051 (part). *J. F. Duthie*.

6. Mugra (prior to 1882), no. 305. *Sir G. Watt*.

Gonda, Oudh, 1921, no. 14. *G. O. Allen*.

9. Sagaing, Upper Burma, 1890. *Abdul Huk*.

Recorded by Braun from (5) Tranquebar and near Madras; (6) Sahebgung, Saharanpore; (8) Assam.

C. brachypus also occurs in Tonquin, the Philippine Islands; in several places in Tropical Africa and in Egypt as far north as Damietta (c. 31° N.): New Guinea; and Northern Australia.

** Gymnopodes.

15. C. ZEYLANICA Willd.

This appears to be distributed over the greater part of Southern and Eastern India, having been collected in many localities in districts 3, 5, and 6, also in (8) Assam, (9) Burmah, (11) Kuala Lumpur, and the Cocos and Andaman Islands.

Recorded by Braun from (3) Nilgiri Hills, (5) Coast of Coromandel, (6) Bengal, (8) Assam, and from Gengu and Busna.

C. zeylanica in one or other of its many forms is very widely distributed in the tropical and subtropical regions of both hemispheres, apparently only reaching beyond the limits of 33° N. and S. of the Equator in the United States of America.

EXPLANATION OF THE PLATES.

PLATE 35.

Nitella mirabilis.

Fig. 1. Portion of ♂ plant, natural size.

2. " ♀ " " "

3. Branchlet-node, ♂. × 15.

4. " " ♀. × 15.

5. Oogonium. × 35.

6. Oospore. × 35.

7. Oospore-membrane. × 200.

8, 9. Tips of dactyls. × 50.

(The magnifications are only approximate.)

PLATE 36.

Nitella Wattii.

Fig. 1. Plant, natural size.

2. Whorl with branchlets. × 6.

3. Single branchlet. × 10.

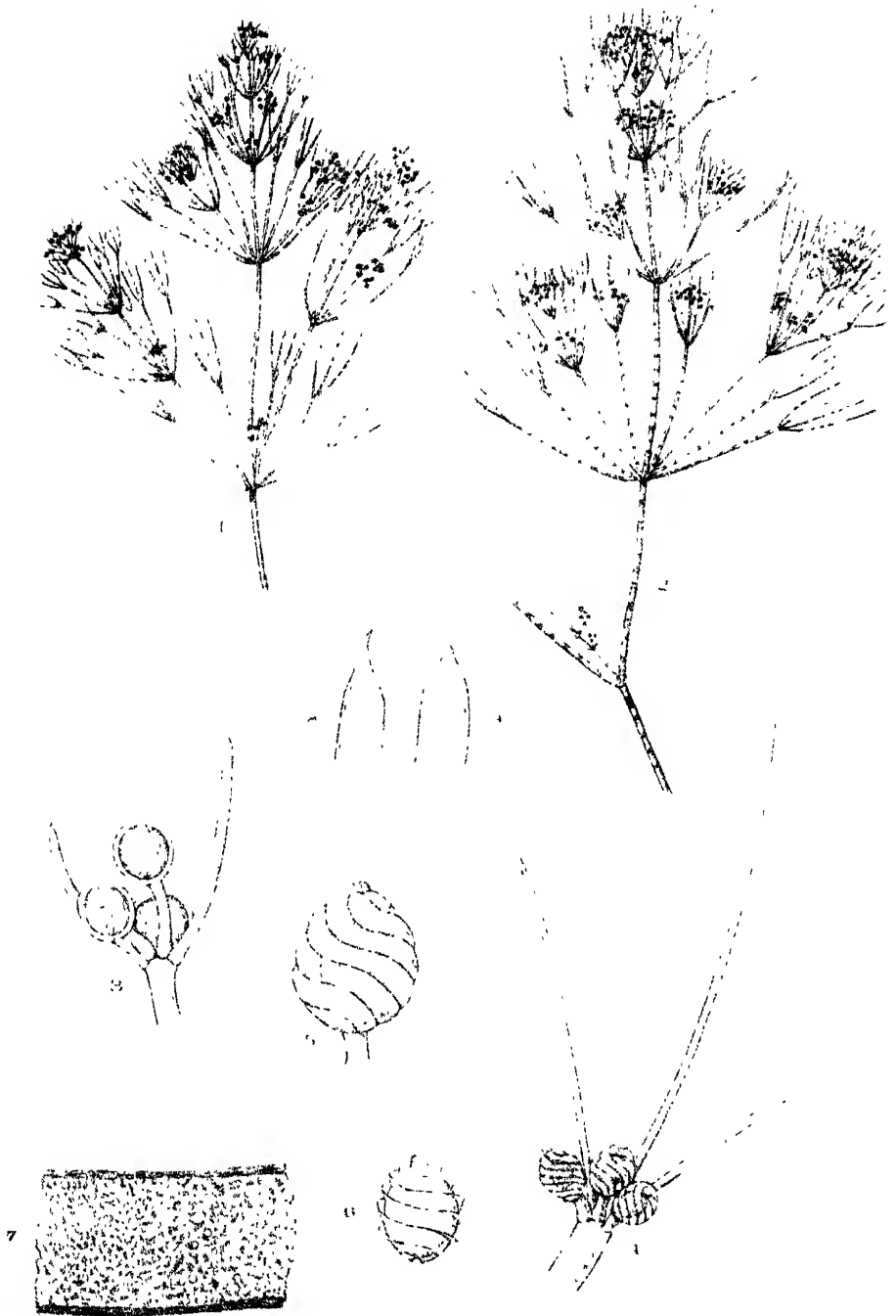
4. Oogonium. × 25.

5. Oospore. × 40.

6. Oospore-membrane. × 350.

7-9. Tips of dactyls. × 125.

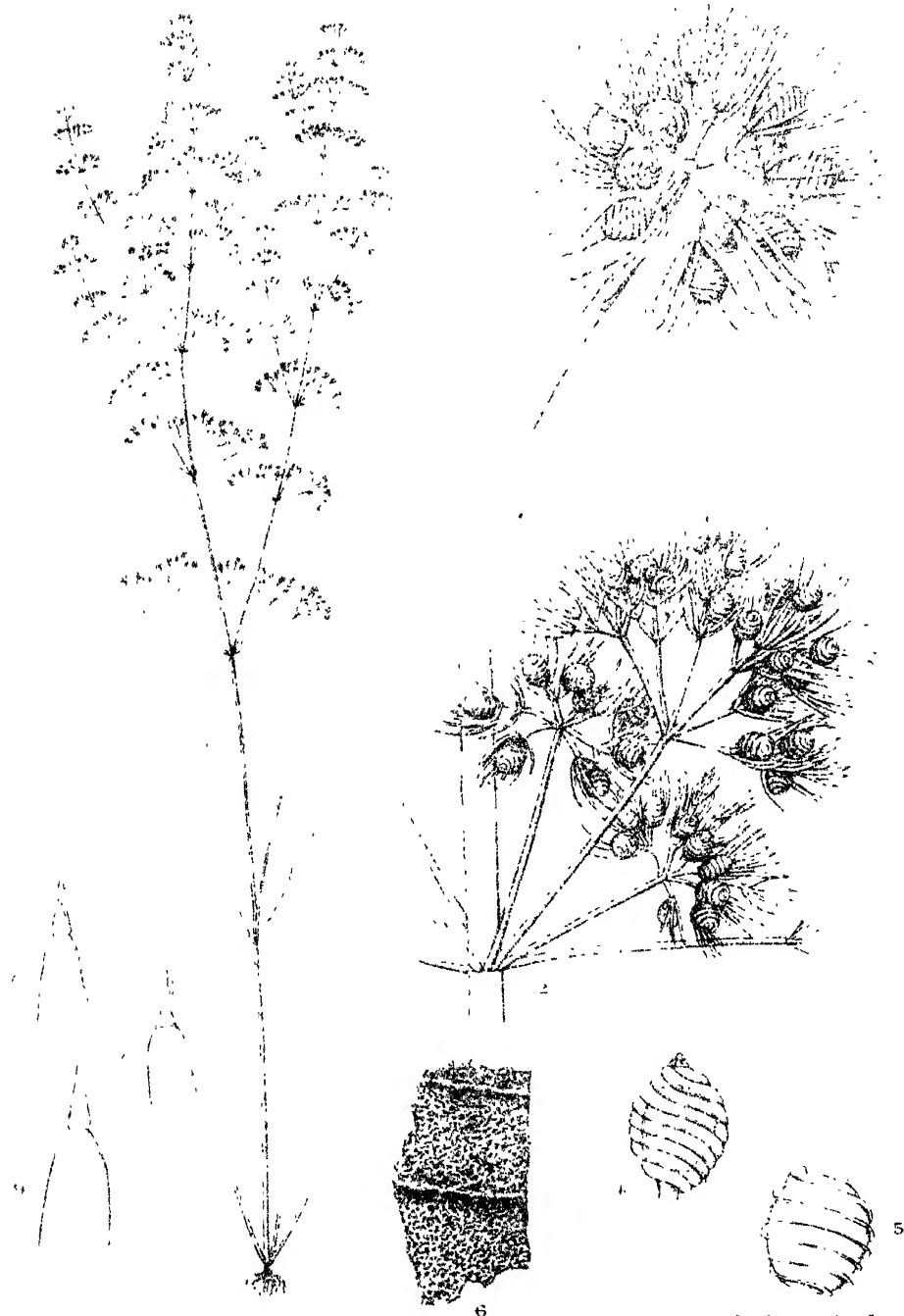
(The magnifications are only approximate.)



M. Groves del
P. Highley lith

NITELLA MIRABILIS sp. nov.

C. Hodges & Co. lith



H&M. Groves. det.
P. Highley. lith.

Highley & Son. Imp.

NITELLA WATTII sp. nov.

On the Cuticular Structure of the Devonian Plant *Psilophyton*. By W. N. EDWARDS. (Published by permission of the Trustees of the British Museum; communicated by J. RAMSBOTTOM, O.B.E., M.A., Sec. L.S.)

(PLATE 37 & 5 Text-figures.)

[Read 1st November, 1923.]

INTRODUCTION.

THE Geological Department of the British Museum (Natural History) possesses several specimens of the Devonian genus *Psilophyton* from Gaspé and other localities in Canada which were collected and presented by Sir J. W. Dawson, and some of which were actually figured by him. This Canadian material presents several points of interest, of which the most important is the presence in some specimens of a cuticle which could be detached from the rock and macerated with Schultze's mixture in the usual manner. The present communication deals with the epidermal structure as seen in cuticular preparations of *Psilophyton princeps* Dawson, one of the earliest land-plants with which we are acquainted.

FIG. 1.



Psilophyton princeps Daws.

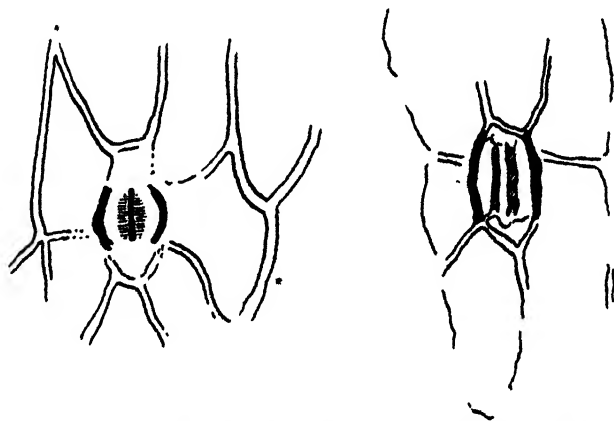
Fragment of stem from specimen V. 14918. $\times 2$.

Most of the specimens dealt with are labelled *P. princeps* var. *ornatum* Daws., but as White (1905, p. 61) and Halle (1916, p. 14) have shown, the so-called variety *ornatum* is really the type of the species, and should henceforth be referred to *Psilophyton princeps*. The best preparations were obtained from specimen V. 14918, a fairly accurate drawing of which was given by Dawson (1871, pl. ix. fig. 100; the figure is natural size). This specimen is a small piece of dark sandstone on which are scattered fragments of the stems of *P. princeps* showing the typical spines or emergences of the species. One of these fragments, about 3 mm. in diameter, is refigured here

(text-fig. 1) and the cuticle shown in Pl. 37. figs. 2, 3, & 6 was taken from it. Several other specimens also yielded cuticles, which were sometimes very fragile and not well preserved, but in all cases where the structure could be made out it agreed with that of the specimen just mentioned. When in Stockholm in the spring of 1922, I examined further material from Gaspé in the palæobotanical section of the Natural History Museum, by kind permission of Prof. T. G. Halle, and obtained good preparations very similar to those in the British Museum.

Before proceeding to describe the specimens in detail, it may be of interest to note that this ancient plant has retained its cuticle practically unchanged since Lower Devonian times, and that no plant cuticles preserved in this way have hitherto been recorded, so far as I am aware, earlier than the Carboniferous. Like other "mummified" fossil cuticles, that of *Psilophyton* takes up stains (such as safranin and methyl green) as readily as if it had been obtained from a living plant.

FIG. 2.



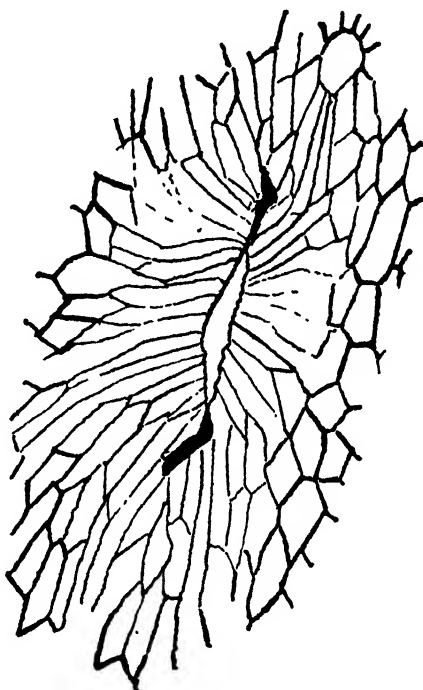
P. princeps. Sketches of stomata from a slide in Stockholm Museum (Palæobotanical Section).

Structure of Epidermis.

The epidermal cells, which are angular and usually longer than broad, vary considerably in size and shape, and Pl. 37. fig. 3 gives a good idea of the variation in a small area. Almost square cells are seen occasionally, but they are more often fusiform or long and narrow with oblique end walls. The actual length of the cells varies from .075 mm. to .3 mm., and the width from .03 mm. to .075 mm. The walls are thick (about .004-.007 mm.) and straight or only slightly curved. The end walls are frequently thicker than the others. There is usually a dark round or oval mark in the centre of each cell, presumably a papilla (see Pl. 37. fig. 2), which is sometimes slightly elongated into a short ridge.

Scattered among the epidermal cells are stomata, whose exact structure is rather difficult to make out (see Pl. 37. figs. 2, 3, 6 & text-fig. 2). They are not very numerous, for there are about 4-9 per square millimetre. They are all orientated in the same direction, with the long axis vertical. They usually appear to have an elongated pore, the walls bounding which are thickened and cuticularised. The outer walls of the cells flanking the pores are also thickened and frequently have a crescentic form. In some cases the pore seems to be closed, and there is only a single dark longitudinal line between the two outer crescentic thickenings (text-fig. 2). It seems

FIG. 3.



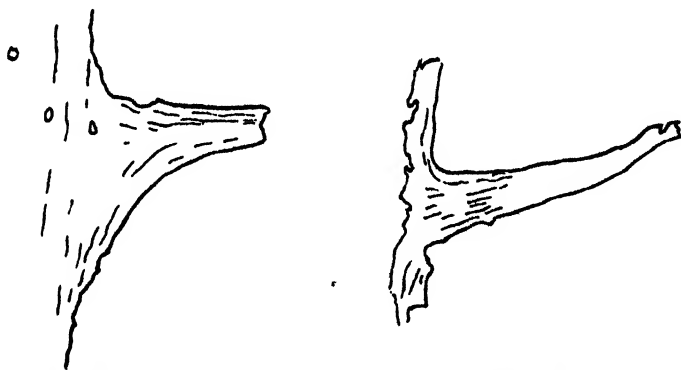
P. princeps. Spine-base from which the spine has been torn away. Slide V. 14918 c, Brit. Mus., Geol. Dept.

probable that the guard-cells were cuticularised along their inner and outer walls, the thinner portions of the walls above and below the pore having disappeared. It is just possible, however, that these cells with thickened walls are subsidiary cells and that the actual guard-cells were on a slightly lower plane and have not been preserved, unless indeed the inner thickenings alone belong to the guard-cells. I have so far been unable to obtain any sections which would throw light on the structure of the guard-cells. As regards their dimensions, the average length of the stomatal apparatus is $\cdot 07$ mm. and the average width $\cdot 03$ mm.

There does not seem to be any definite arrangement of the cells round the stomata, which vary in number from 4 to 7, but their walls are sometimes rather fainter than those of the ordinary epidermal cells. In some instances these cells appear to be very slightly below the general level of the epidermis, as if they formed a very shallow pit containing the stoma, but on the whole the thickened ridges of the stomatal apparatus seem to be on the same plane as the rest of the cuticle.

The Emergences.—The spine-like emergences which are so characteristic of the species have usually disappeared from the flattened part of the stem, leaving a slit or oval space in the cuticle (indicating that the spines were flattened vertically) around which the radiating epidermal cells tend to be rather elongated. Part of one of these spaces from which a spine has been torn away is shown at the top of fig. 2 (Pl. 37) and another in text-figure 3. A few preparations were made of spines attached to the edge

FIG. 4.



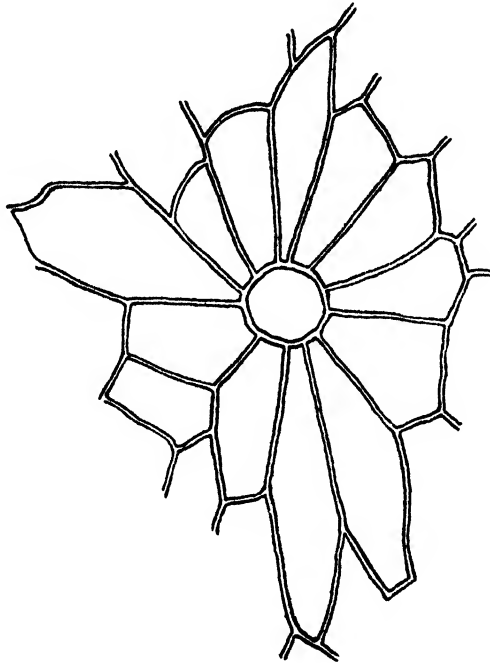
P. princeps. Spines; left, shows a stoma close to the base, slide V. 678 a; right, slide V. 678 b, Brit. Mus. Geol. Dept.

of the flattened stem (text-fig. 4) showing their tapering form with occasionally a well-marked longitudinal striation, while especially near the tip they were of a much darker colour than the epidermal cells, as if they were highly cuticularised. No stomata nor veins were seen on the spines examined, and rarely any trace of cell-walls, except near the base. The use of the term "emergence" rather than "leaf" would therefore seem to be justifiable, and even if they are to be regarded as rudimentary leaves—the starting point of the leaf of the microphyllous Pteridophytes—it seems clear that in *Psilophyton princeps* they were not concerned with assimilation. Since the tip was so fine and pointed, it was difficult to obtain exact measurements, but apparently the spines did not exceed 2.5 mm. in length in the material at my disposal, and were often shorter. Sections of the spines showed only that they were vertically flattened and that they were very thin.

In addition to the scars of the macroscopic emergences, there are certain arrangements of the epidermal cells (see Pl. 37. figs. 2 & 3 and text-fig. 5), in which a small circular central cell or space is surrounded by elongated radiating cells. These much resemble the hair-bases of many higher plants, and *Psilophyton* may therefore have been provided with a few scattered hairs in addition to the larger spines. These supposed hair-bases are very much smaller than the spine-bases, and there does not appear to be any intermediate stage between the two. No hairs have been seen attached to the bases.

Text-figure 4 shows a stoma close to the base of a spine, but there is no definite or regular association of stomata and emergences.

FIG. 5.



P. princeps. Hair-base (?). From a slide in the Stockholm Museum.

Before proceeding to a discussion of the significance of these features of the cuticular anatomy, it may be noted that no satisfactory epidermal preparations have so far been obtained from the axes of the fructifications (*Dawsonites arcuatus* of Halle) nor from the smooth-stemmed "Campbelton" type described as *Psilophyton* by Dawson. It may be suggested, as a possibility to be borne in mind, that some of the smooth-stemmed forms may be a different state of preservation, having undergone a certain degree of decortication before being fossilised.

Comparisons with other Specimens.

In comparing the present material with previously described examples of *P. princeps* we naturally consider first Dawson's figures and descriptions. We are not here specially concerned with the plant as a whole nor with its supposed rhizomes and fructifications, but in order to give a clear idea of the external appearance of the stems as they occur at Gaspé one of Dawson's specimens is reproduced on Pl. 37. This is the slab (or possibly its counterpart) partly figured by Dawson (1871) on pl. 9. fig. 97. It may be noted that in his drawing the spines are occasionally shown as rather stouter structures than is justified by the appearance of the actual specimen. The longest piece of stem I have seen (incomplete at each end) is 18 cms., and the British Museum specimens do not exceed 5 mm. in breadth, except at the point of branching. Dawson states (1871, p. 39) that "after the removal of the leaves the stems exhibited rounded spots somewhat irregularly arranged, indicating the slender bundles of vessels passing to each leaf." The minute spine scars do not seem to me, however, to warrant the statement that vascular bundles ran out to the "leaves." When the actual cuticle is present the scars are often merely round or oval lacunæ, and in the casts there is usually only a little tubercle to be seen (or a depression in the case of moulds, sometimes filled with a fragment of cuticle which thus makes a black spot on the impression), and I have not observed any central spot which might be interpreted as a vein-scar.

Dawson does not mention stomata in his description, but figures (1871, pl. 11. fig. 129 a) a "portion [of a leaf] more magnified, showing cellular structure and a stoma." There is nothing in the drawing, unfortunately, which bears any particular resemblance to a stoma, and as stated above I have not been able to confirm the presence of stomata on the spines.

The species has been recorded from various localities, and among the figures given by Halle (1916) of material from Norway are two (pl. 2. figs. 3 & 5), showing a "sculpture of the outer surface" which Halle tentatively regards as representing the epidermal cells. A comparison with the cuticle described in the present paper confirms this, and the average breadth of the cells is the same in each case. The stems of the Norwegian specimens are larger than the Canadian material in the British Museum, sometimes having a diameter of 10 mm., but the spines are about the same size.

A specimen of *P. princeps* from the Lower Old Red Sandstone of Perthshire, has recently been figured by Mr. J. Walton (1923, pl. 9. fig. 12) in illustration of his new method of preparing fossil plants. His specimen shows the spines very clearly but not the cellular structure of the epidermis. Since the spines were better preserved than the rest of the plant, Walton concludes that they were more highly cuticularised, and suggests that "they were probably not structures representing an extension of the area of protosynthetic tissue, and that if they had any function at all it was of a

mechanical nature." This is in agreement with the conclusions arrived at in the present paper.

Comparisons with Rhynia and Asteroxylon.

The exact relationship of *Psilophyton* to the primitive Pteridophytes of the Rhynie Chert has been much discussed since Kidston and Lang instituted the class Psilophytales for their reception, taking the name from Dawson's genus. Kidston and Lang (1917) at first regarded the affinity of *Rhynia* with *Psilophyton* as fairly close, and Arber (1921) went so far as to state that the two genera were identical. In their later work Kidston and Lang (1920, p. 669) consider that *Psilophyton* is more closely comparable with *Asteroxylon*, and they include it in the family Asteroxylaceæ. They do not suggest generic identity, and indeed among known impressions there is one which vegetatively resembles *Asteroxylon* much more closely, namely *Thursophyton*. The other Rhynie genus, *Hornea*, need not detain us, since its epidermis is not very well known and it had no emergences of any kind and apparently no stomata.

The epidermal cells of *Rhynia* and *Asteroxylon* agree on the whole in shape and dimensions, and those of *Psilophyton* are very similar, but often more elongated than in these two genera. The dark median ridge of the cells of *Rhynia Gwynne-Vaughani* (Kidston and Lang 1917, pl. 6. fig. 31) which is sometimes also seen in *Asteroxylon* is usually represented in *Psilophyton* by a round or only slightly elongated papilla, but there is occasionally a line running nearly the whole length of the cell. In the case of *Rhynia major* there are no ridges on the epidermal cells.

The stomata of *Rhynia* are similar to those of *Asteroxylon* and are of ordinary form consisting of two crescentic guard-cells apparently without any special thickening, whereas in *Psilophyton* the cuticular thickenings suggest a more specialised type of stoma. In the latter genus the stomatal apparatus seems to be narrower and often longer than in the Rhynie plants, but this might be due to differences in the state of the stoma at the time of fossilisation. On the whole the stomata are more numerous than in *Rhynia*, and in this respect *Psilophyton* agrees better with *Asteroxylon*, of which a piece of cuticle with about a dozen stomata is shown in Pl. 37. fig. 5 for comparison. A few stomata are rather more highly magnified in fig. 4, but though they do not closely resemble those of *Psilophyton*, it must be remembered that the method of preservation is very different.

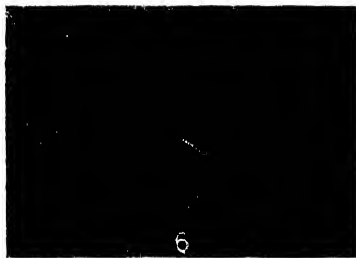
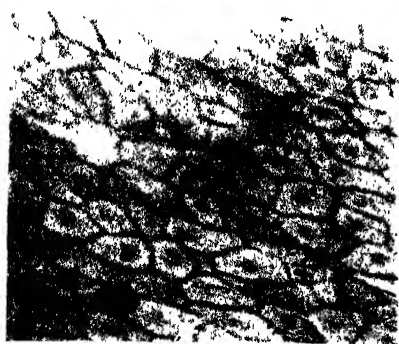
The arrangements of cells described above as hair-bases have not been seen in either *Rhynia* or *Asteroxylon*. There remain the emergences to be considered. The hemispherical protuberances of *Rhynia Gwynne-Vaughani* have been shown by Kidston and Lang to be usually if not always formed underneath a stoma, and it is highly probable that they were a traumatic response to the peculiar conditions under which the plant lived. They may

possibly have been due to the presence of irritating vapours from fumaroles, and in any case did not form part of the original equipment of the plant. There is no close resemblance between these intumescences composed of thin-walled cells, and the highly cuticularised spines of *Psilophyton*, which are not definitely arranged in relation to stomata. Arber (1921, p. 25, fig. 7) laid much emphasis on the supposed resemblance between an axis of *Rhynia* figured by Kidston and Lang showing the external surface with intumescences and a fragment of *Psilophyton* figured by Halle (see above) showing spine-bases. It is to be noted that in the latter the actual spines were not present and that the radiating arrangement of epidermal cells round the spine-bases (shown in Halle's figure) is not found in the case of the *Rhynia* outgrowths. We have already seen that the general resemblance of the epidermal cells of *Rhynia* and *Psilophyton* extends also to *Asteroxylon*. The structure of the epidermis and emergences does not, therefore, suggest such a very close relationship between *Rhynia* and *Psilophyton* as was claimed by Arber. The emergences of *Psilophyton* are more like the simple leaves of *Asteroxylon* in appearance, but there are important differences: the leaves of the latter, which are larger and are sometimes nearly 1 cm. in length, are provided (though sparingly) with stomata, and sections as figured by Kidston and Lang (1920, pl. 5, fig. 39) show a papillate epidermis, whereas the spines of *P. princeps* are perfectly smooth. In *Asteroxylon* there is an extension of cortical tissue into the leaf, though the leaf-trace only reaches to the base and does not run into the free portion, but the spines of *P. princeps* seem to be so highly cuticularised and so slender that there can have been very little cortical tissue in them, if any.

Though there are differences in the epidermal structure which may be of importance, the above comparisons support on the whole the view that *Psilophyton* is more nearly related to *Asteroxylon* than to *Rhynia*. This view was based by Kidston and Lang on the general organisation of *Psilophyton*, but the internal anatomy of the genus is not yet sufficiently known for a decisive answer to be given to the question of its exact systematic position. Comparisons with other early Devonian impressions are not at present possible, and attempts to macerate specimens of *Thursophyton* and other Scottish Old Red Sandstone plants have not so far met with success.

Summary.

An investigation of the cuticle of *Psilophyton princeps* Dawson from the original locality in Canada has revealed the presence of stomata on the epidermis of the stem. This epidermis resembles in a general way that of the petrified members of the *Psilophytales* from the Rhynie Chert, but the stomata differ in the presence of cuticular thickenings and the epidermal cells are usually papillate and not ridged. In the numerical distribution of stomata on the stem, *Psilophyton* agrees with *Asteroxylon* rather than *Rhynia*. There



PSILOPHYTON Daws. and ASTEROXYLON Kidst. & Lang.

is no evidence that the highly cuticularised spines are homologous with the traumatic intumescences of *Rhynia*, and they differ from the slightly larger and less spine-like leaves of *Asteroxylon*, with which a closer comparison is possible, in the absence of stomata.

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EXPLANATION OF PLATE 37.

- Fig. 1. *Psilophyton princeps* Daws. Gaspé, Canada. $\frac{2}{3}$ nat. size. Brit. Mus. Geol. Dept., no. V. 13233. Photo H. G. Herring.
 3. *P. princeps*. Cuticle with stomata taken from the fragment shown in text-fig. 1. $\times 52$. Slide V. 14918c. Photo J. H. Leonard.
 2. *P. princeps*. Another portion of the same cuticle, showing papillæ. $\times 75$. Photo F. W. Edwards.
 6. *P. princeps*. A single stoma from the same slide. $\times 240$. Photo F. W. Edwards.
 5. *Asteroxylon Mackiei* Kidst. & Lang. Rhynie Chert, Old Red Sandstone, Aberdeenshire. Epidermis with stomata. $\times 30$. Slide V., Brit. Mus. Geol. Dept. Photo F. W. Edwards.
 4. *A. Mackiei*. Part of the cuticle shown in fig. 5. $\times 60$. Photo F. W. Edwards.

The *Onosmas* of Linnæus and Sibthorp, with a Note on those of Tournefort's Herbarium. By C. C. LACAITA, M.A., F.L.S.

(PLATE 38.)

[Read 29th November, 1923.]

I.

THE name *Onosma* has sometimes been treated as feminine; so by Linnæus, De Candolle, and others; sometimes as neuter, as by Lehmann, Boissier, Bentham and Hooker, Ind. Kew. etc., the neuter prevailing in modern works. In what follows I have used the neuter throughout, even when quoting authors who employed the feminine. As to the merits, *ὄνοσμα* is, of course, neuter in Greek, but Linnæus probably thought that he was following Pliny, xxvii. 86: "*Onosma longa folia habet . . . prægnans si edit EAM . . . abortum facere dicitur.*" There is an ambiguity; it must remain uncertain whether Pliny would really have made *Onosma* feminine, or we should understand *eam* as equivalent to *eam herbam*.

II.

THE SPECIMENS OF *ONOSMA* IN TOURNEFORT'S HERBARIUM AT PARIS.

In the 'Institutiones,' p. 138, there are enumerated three species of *Symphytum*, now transferred to *Onosma*; these are:—

- (1) *S. Echii folio ampliore, radice rubra, flore luteo*, syn. *Anchusa lutea*, major C. B. P. 255, *Anchusa lutea* J. B. 3. 583, Lob. Icon. 578.
- (2) *S. Echii folio ampliore, radice rubra, flore exalbido*, with syns. *Anchusa flore albo aut pallido Clusii* J. B. 3. 383 and *Anchusa exalbido flore* Clus. Hist. clxv.
- (3) *S. Echii folio angustiore, radice rubra, flore luteo*, with syns. *Anchusa lutea minor* C. B. P. 255, *Anchusa echiioides lutea, cerinthoides montana* Col. Pars i. 183.

Of these only two, the first and third, are to be found in the herbarium. One, no. 629, *sine loco*, labelled *Symphytum Echii folio angustiore, radice rubra, flore luteo*, Inst. *Anchusa echiioides lutea cerinthoides montana*, is—so far as can be judged from an incomplete specimen without lower leaves or root—the asterotrichous plant common in the Apennines, first discovered by Fabio Colonna, the true *O. echiioides* α of Linnæus. The other, no. 628, also *sine loco*, labelled *Symphytum Echii folio ampliore, radice rubra*, but without the addition of *flore luteo* or *flore exalbido*, is haplotrichous and evidently the *Onosma echiioides* of French authors = *O. echiioides* β of Linn. *quoad plantam ex Gallia*, corresponding to no. 1 of the 'Institutiones.'

In the 'Corollarium,' pp. 6 and 7, ten more species of *Symphytum* are added, of which we need only consider two, none of the others being represented in the herbarium. One of the two is *Symphytum Creticum*, *Echii folio angustiore, longissimis villis horrido, flore croceo*, sheet no. 629, *sine loco*. It is certainly *Onosma græcum* Boiss., as Bonnier has noted on the sheet. The other, *Symphytum Orientale*, *Oler folio cinereo et hirsuto*, is represented by specimen no. 632, although the ticket, in Tournefort's own hand, substitutes the word *ponticum* for *Orientale*, a variation that need not trouble us. The locality is "Proche Penderuchi sur la mer noire." In the 'Voyage du Levant,' p. 183 (ed. 1717), the author tells how on May 1st, 1701, he reached Penderachi, better known as Bender-Eregli, and in ancient times as Heraclea Pontica: the port where Xenophon embarked the survivors of his 10,000 on their return voyage to Greece. That this place is on the coast of ancient Bithynia rather than Pontus need not trouble us any more than the fluctuation of the name between *orientale* and *ponticum*. The specimen is *Onosma albo-roseum* Fisch. et Mey. (1839), a beautiful Anatolian species. It must, however, henceforth bear the earlier name *O. cinereum* Schreb. (1767), which has hitherto been taken to indicate one of the forms included in or allied to *O. echioides* L.f., through confusion with the later and invalid *nomen nudum* *O. cinereum* Sieb., under which name Sieber distributed both *O. erectum* Sibth. et Sm. from Crete and the closely-allied *O. angustifolium* Lehm. from Apulia. Dr. H. Ross, the Curator of the Munich Herbarium, has kindly inspected Schreber's type-specimen, which lies there. It had been collected by Tournefort in the east, and bears the label or writing "lecta a Tournefort in Ponto." This origin, combined with the "corolla purpurea" and other characters of Schreber's description, make it clear that it is identical with specimen no. 632 at Paris and with *O. albo-roseum*, as has already been suggested by Rübel and Braun-Blanquet in Vierteljahrsschr. Nat. Ges. Zürich for 1917, p. 608.

III.

ONOSMA IN LINNÆUS.

The second edition of 'Species Plantarum' enumerates three species of *Onosma*, only one of which had been mentioned, under the name of *Cerinthe echioides*, in the first edition. The herbarium, however, contains two specimens, unnamed by Linnæus, of a fourth species, *O. tinctorium* M. Bieb., but none of *O. orientale*, the Syrian plant for which Boissier, *Diagn. Ser. 1, xi. p. 113* (1849), created the genus *Podonosma*. Taking the species in order:—

(1) *O. TINCTORIUM* M. Bieb. Although not mentioned in Linnæus's works, this is represented in the herbarium by specimens no. 2 and no. 3, both unnamed by Linnæus. They are *sine loco*, but are both marked \mathfrak{D} -, signifying that they were received from Gmelin.

(2) *O. SIMPLICISSIMUM*. "Habitat in Sibiria. Gmelin." There are two specimens; no. 1, labelled, "*simplicissima*" by Linnæus and marked -E as sent by Gerber (not Gmelin), and therefore coming from South Russia, not Siberia; also no. 4, marked Θ- as coming from Gmelin. This no. 4 has not been named by Linnæus; it is composed of small pieces, parts of a larger plant, and is unquestionably *simplicissimum*, though Smith has pencilled, but afterwards cancelled, "*echioides a*," to which these pieces bear no resemblance.

(3) *O. ORIENTALE*. "Foliis lanceolatis hispidis, fructibus pendulis. *Cerinthe orientalis* Amœn. acad. iv. 267. Habitat in Oriente." The words *fructibus pendulis* point clearly to a *Podonosma*, but to which of the two known species—the Syrian *P. syriacum* (Labill.) Boiss., or the Egyptian *P. galatense* Schweinf. in Boiss. Or. iv. p. 1198? In Am. Ac. loc. cit. (Cent. I. no. 16) a fuller description is given, and the plant is said to have been collected by Hasselquist "in Aegypto." On the other hand, in the 'Flora Palæstina' *Cerinthe orientalis* is catalogued as collected by Hasselquist in Judæa (Am. Ac. iv. p. 452). Now, although the Linnean herbarium does not contain *O. orientale*, there is a specimen in Hasselquist's collection at Upsala which Dr. Juel has identified as *Podonosma syriacum* in spite of the sheet having nothing written on it except the letters "aeg." evidently signifying "Aegyptus." A photograph which Dr. Juel has kindly sent me (and which is here reproduced, Pl. 38) entirely confirms this determination. He writes: "I do not think that the letters *Aeg.* were written by Hasselquist . . . in my opinion it is probable that Thunberg wrote *aeg.* on this and many other specs. in this collection, and that he only meant to say that the specimen belongs to Hasselquist's collection of oriental plants, which he signifies indiscriminately as Egyptian." Indeed, it is most improbable that Hasselquist should have visited so out-of-the-way a spot as the caves of Wady Natfe, where Schweinfurth found *Podonosma galatense*. Moreover, in Am. Ac. there is quoted as an uncertain synonym "*Symphytum orientale echii folio minori* Tourn. Cor. 6?". There is no specimen of this in Tournefort's herbarium, but it could not have been Egyptian.

It must not be overlooked that Boissier, Fl. Or. iv. p. 1199, says "*Onosma orientale* ex herbarii Linneani inspectione est *O. stellulati* W. K. forma," but he is referring to specimen no. 5, which represents not *O. orientale* but *O. echioides*, and will be discussed below.

(4) *O. ECHIOIDES*. This is the only Linnean species that still presents any difficulty. Linnæus was well aware of the inadequacy of his treatment of it, for in his own copy of Sp. Pl. ed. 2 he has written against *echioides*, "här är flere species"—"here are many species." His first mention of the more or less closely-related forms which have laid claim to the specific name is in Hort. Cliff. p. 48, as *Cerinthe foliis lanceolato-linearibus hispidis*, with Austria

and Pannonia as habitat and four synonyms, of which only the third, *Anchusa exalbido flore* Clus., a haplotrichous species, is found in those lands. The specimen in Herb. Hort. Cliff. is haplotrichous, but being incomplete and obviously from cultivation, it would be rash to decide to which of the haplotrichous forms that, as we shall see, are comprised in *echioides* β of Linnæus it should be referred. As far, therefore, as Hort. Cliff. is concerned, a haplotrichous *Onosma* is signified, notwithstanding that the three other synonyms, (1) *Symphytum echii folio angustiore, radice rubra, flore luteo* Tourn., (2) *Anchusa lutea minor* C. B. P., and (3) *Anchusa echioides lutea, Cerinthoides montana* Column., all belong to a totally different species, the well-known asterotrichous plant of the Apennines, of which I shall speak as Columna's *Onosma*, because it was first observed by Fabio Columna "in saxosis Aequicolorum montibus," the country of the Aequicoli, now known as the "Cicolano" in the Abruzzi, lying N.W. of the now drained bed of the Lago di Celano (Lacus Fucinus), and by him described and figured in the first edition of his 'Ecphrasis' (1606), pp. 182, 183.

When we come to the Spec. Plant. of 1753 we find the same two plants, still under the genus *Cerinte*, but no longer lumped together. Now they are clearly separated into α (though Linnæus as in many other cases does not mark as α the plant first spoken of) and β . The only alteration in ed. 2 is the transfer from *Cerinte* to *Onosma* and the addition of the inadequate diagnosis *O. foliis lanceolatis hispidis, fructibus erectis*, which, like the Hort. Cliff. synonym, applies indifferently to α and to β , and would cover sundry other species as well.

Unfortunately, later authors have considered themselves at liberty to use the name *echioides*, without any qualification, for α or for β according to their own fancy, without following any principle. The result has been such confusion that many moderns would like to abandon the Linnean name altogether, though its abandonment has only led some of them deeper into the mire. The principle is surely quite clear that when Linnæus distinguishes an α and a β and the identity of each can be definitely ascertained, it is α that has the absolute right to the exclusive use of the specific name without qualification. There are indeed instances in which the Linnean β has by general consent and uniform practice been allowed the priority, but in each instance for some special reason such as does not exist in the present case. Unluckily, Linnæus has not distributed between α and β respectively the various habitats mentioned—Austria, Pannonia, Helvetia, Gallia, Italia. Had he done so it is probable that much confusion would have been avoided, for α is only found in Italy and Dalmatia, while β exists in some form in all the other lands in which α is unknown.

(NOTE.—I do not include *O. helveticum* under either α or β , as it is, in my opinion, to be specifically distinguished from Columna's *Onosma*; *O. vaudense* belongs to β .)

We must now proceed to further identification of α and β . In Spec. Plant. there follow after the Hort. Cliff. synonym, which includes both α and β , two others, referable to α alone, that are perfectly clear and absolutely decisive. They are *Anchusa lutea minor* C. B. P. and *Anchusa echioides lutea, cerinthe* (sic) *flore, montana*, Column. On reference to C. B. P. we find that his *Anchusa* III., *lutea minor*, has for its sole synonym *Anchusa echioides lutea* Column., and in my preceding note on Tournefort's specimens it has been indicated that the Tournefort synonym quoted in Hort. Cliff., but not in Sp. Pl., is precisely Columna's plant. It is therefore Columna's *Onosma*, as the sole representative of the Linnean *echioides* α , that is entitled to the specific name *echioides*.

This view has already been clearly stated by Wettstein in Sched. ad Fl. Exs. Austr. Hung. no. 1411 (1886), after which it was to be hoped that it would be universally accepted, as it has been by Jávorka in his excellent paper on the "Species Hungaricæ generis *Onosma*" in Ann. Mus. Nat. Hung. (1906). It is therefore dis-appointing to find it ignored by Rübel and Braun-Blanquet in their recent paper, "Zur Kenntniss der mitteleuropäischen *Onosma*-Arten"—most valuable for the forms of Switzerland and neighbouring regions,—in Vierteljahrsschr. Nat. Ges. Zürich, lvii. (1917), where they have followed Boissier and the French school in using the name *echioides* L. for the portion of the β of Linnæus. They have moreover introduced a fresh confusion on p. 604 by identifying *O. arenarium* Waldst. et Kit. with *echioides* α instead of with β , and have even been so careless as to quote the reference as Spec. Plant. ed. 1, p. 137 (1753). Is it conceivable that they can have looked up that page without noticing that *echioides* there occurs under *Cerinthe*, not *Onosma*? It is a pity that bibliographical remissness should disfigure their otherwise careful study.

It is also unfortunate that Simonkai, reviewing Jávorka's paper in Mag. Bot. Lapok, v. (1906), set up a new, worse than superfluous, name as follows: "*O. Jávorkæ* Simonk. = *O. echioides* Jávorka et Fl. Exs. Austr. Hung. 1911. *Anchusa* Columnæ ex habitu, sed neque ex icone neque ex descriptione ejus apparet foliorum asterotrichia, nec corollæ pubescentia." All this quibble only shows ignorance of Columna's plant, which is proved by the specimens from the *locus classicus* to have pubescent corollæ and an asterotrichous indumentum. The figure agrees with the specimens as well as most old figures do, the size and manner of Columna's drawings usually giving the impression of plants being smaller than they really are. Simonkai's "nomen supervacaneum," as Halácsy has called it, would be peculiarly inappropriate even if a new name were required, for with the specimens distributed in Fl. Exs. Austr. Hung. Jávorka had nothing to do. It would have been more reasonable to have called them *Wettsteinii*. There is a further quibble about these specimens to be dealt with. They are not perfectly uniform; no. II. from Trieste is not distinguishable from the typical plant of Columna's

country, but no. I. is a broader-leaved variety that occurs frequently in Dalmatia and occasionally in some parts of Italy, to which Scheele in 1843 gave the name of *O. dalmaticum*.

Through the kindness of my friend Signor Loreto Grande, whose home is in Columna's country, I have seen sufficient specimens, both from the Cicolano itself and from Villavallelonga south of the old lake, to feel sure that Columna's plant is identical with the *O. montanum* of Ten. Syll. p. 85 (*non* Sibth. & Sm.), which I know well in other parts of southern Italy and which Sir J. E. Smith collected at Valcimara in the Marche, 136 miles north of Rome, on April 29th, 1787, and at once recognized as "*Onosma echiioides* Column. Ecphr. 183, which seems to be a distinct species from the Linnean variety β found about Montpellier, being less hairy and the bristles on the leaves are curiously stellated at their bases" (see Smith's 'Sketch of a Tour on the Continent,' p. 308, ed. 1793).

Sundry Italian botanists have hesitated to use the name *echiioides* for this species, and have called it *stellulatum* Waldst. et Kit., which is altogether wrong, or *cinereum* Schreb., which is still more wrong, or *montanum* Sibth. et Sm., a pitfall into which they have been decoyed by Smith's later mistake in Prodr. Fl. Græc., of which more below. *O. angustifolium* Lehm. would be nearer the mark, as it is the name given by Lehmann to a very closely-related form, confined to Apulia, where it was first collected by Sieber and which I regard as a subsp. or variety of Columna's *Onosma*.

It is unfortunate that the Linnean herbarium does not give us more help towards the identification of *echiioides* α . It contains only one asterotrichous specimen of *Onosma*, no. 5, originally labelled by Linnæus, in ink that is now very faint, "*Cerinthe orientalis echiioides?*" and relabelled by him at some later date in darker ink, "*echiioides*"; he has also written *a tergo* "*Symphytum orientale flore luteo*." The only other writing on the sheet is an abbreviated word, which may refer to the locality whence the plant came or to the correspondent who sent it; but it is so illegible that even Dr. Daydon Jackson is unable to decipher it. The original reference of the specimen to *Cerinthe* points to Linnæus having received it before he created the genus *Onosma*, and the *orientalis* both on the back and the front to the origin being Asiatic. *Symphytum orientale flore luteo* was probably intended to refer to one of the oriental species mentioned in Tournefort's 'Cérollarium', but that precise name does not occur there. There can be little doubt that the specimen is Anatolian; it is certainly not Columna's species nor, as Boissier thought, *O. stellulatum* Waldst. et Kit., but agrees exactly with the very strigose form of *O. pallidum* Boiss. which is found near Smyrna. It so happens that it is identical with the unique specimen of *O. montanum* in herb. Sibthorp, which, as will be explained below, is not the plant published under that name by Smith in Fl. Gr. Prodr. Its only claim therefore to represent *echiioides* α lies in the strongly asterotrichous indumentum. Smith

has pencilled on the sheet "*O. orientalis?*", which may have led Boissier—as already pointed out—to suppose that the specimen stands for *O. orientalis* L., with which it has nothing to do ; indeed, Linnæus expunged the *orientalis* in his later writing on the sheet.

In my "*Piante Italiane Critiche*," no. xciii. (in *Nuov. Giorn. Bot. It.* xxxiv. pp. 26–29, 1924) I have arranged as follows the Italian forms which may be united under *O. echioides* as varieties ; they are all alike in their perennial root and strong woody base ; in their preference—not exclusive—for limestone ; in their simple or slightly branching stems ; in their astero-trichous indumentum ; in their usually very narrow leaves ; in their sessile fruiting calyces, a character which completely separates them from *stellatum* Waldst. et Kit. and less markedly from the *helveticum* group ; and in their very small shiny nuckles.

(A) var. *Columna* mihi = *O. echioides* L. sensu strictissimo = *O. montanum* Ten. Syll. = *O. Jarovka* Simonk. p. parte. From a woody branched trunk spring tufts of leaves and simple flowering stems, 15–30 cm. high, which bifurcate above the middle. Indumentum usually spreading ; leaves setoso-tuberculate, linear, 2–3 mm. wide, with revolute margins, the uppermost broader (8 mm.) at the base, and sometimes semiamplexicaul ; the starry bristles (asterosetulae), which are disposed in a circle round the base of the stronger bristle that crowns the tubercle, usually completely covering and concealing the surface of the leaf, thereby giving a grey aspect to the foliage *in sicco* ; fruiting calyces sessile ; corolla pale waxy yellow, 2–2½ cm. long, puberulent, and with very minute scattered lemon-coloured glands ; free part of filament equalling the length (c. 6 mm.) of the small anthers. Nuckles very small (c. 2½ mm.). *Habitat* : the Apennines from southern Calabria to the Marches, reappearing near Trieste and in Istria.

(B) var. *dalmaticum* mihi = *O. dalmaticum* Scheele, in *Flora*, xxvi. p. 561 = *O. Jarovka* Simonk. quoad exempl. ex Dalmatia. This form seems to preponderate in Dalmatia. Scheele described it from specimens collected by Petter near Spalato and distributed in 1830. It is very variable, but only differs from var. *Columna* in the broader flattish leaves, hardly or not at all revolute at the margins, in the taller stems, and in the darker colour of the foliage *in sicco*, due to the more widely-spaced stellæ allowing the leaf-surface to show between them. This variety is sometimes as hairy as var. *Columna*, and more often much barer, in a form which I have called *forma calrescens*, especially in the Abruzzi and in Dalmatia.

(C) var. *veronense* mihi = *O. angustifolium* of Rigo's exsicc. and of Fl. Ital. Exs. no. 939 (in synonymy), not of Lehmann. This has the

narrowest leaves of all, only 1–2 mm., the upper ones not being dilated at the base. Otherwise it resembles var. *Columnæ*, but differs from true *angustifolium* Lehm. in the darker grey colour of the foliage, the even narrower leaves, and the weaker, more hair-like bristles, which are spreading, not adpressed. It is confined to the province of Verona, on the hills near the lake of Garda, and by the Adige. All the specimens seen were collected by Rigo, and are very uniform.

- (D) var. *angustifolium* mihi = *O. angustifolium* Lehm. = *O. cinereum* Sieb. (non Schreb.) quoad exsicc. ex Apulia. Stem more dwarf; foliage ashy or whitish in *sicco*, owing to the white bristles being stouter and more adpressed; the surface of the leaves, which are 2–2½ mm. wide, completely concealed by the almost interlacing *asterosetulae*; corolla pale, of a creamy colour, minutely pubescent. But for the presence of this fine pubescence the variety would be practically indistinguishable from the Cretan form of *O. erectum*, of which it has the habit. Lehmann described his species from Sieber's exsicc. ex Apulia, of which there is an example at Mus. Brit. identical with Porta and Rigo's specimens and with those I have myself collected on Mt. Gargano, the only known *habitat* for this precise variety.
- (E) var. *crinitum* mihi = *O. stellulata* var. *crinita* Boiss. herb. in sched. ined. = *O. canescens* Presl = *O. montanum* Guss. non. Sibth. et Sm. Peculiar to Sicily, where it is the only representative of *O. echioides*. Presl's name was ill-chosen, for the plant is flavescent rather than canescent, at any rate in *sicco*. As indicated by Boissier's unpublished name, it is more shaggy than other varieties, the stem being thickly covered with spreading bristles longer than its diameter. The leaves are completely covered by the *asterosetulae*; the corolla is more pubescent and of a deeper yellow than in the others.

When we come to consider *O. echioides* β the case is different. There is no one particular haplotrichous form that can claim to represent β to the exclusion of others, for both the synonyms and the geography cover a whole group of closely-related species or subspecies that have never yet been treated in a convincing manner, not even in the papers of Jávorka and Rübel and Braun-Blanquet. None of these authors have dealt with the entire series and consequently have not faced all the problems.

We cannot avoid including under β at least all the following; this is not the place to discuss their precise relationships:—

- (1) *O. Visianii* Clem. (1842) = *O. calycinum* Stev. (1851) from Hungary and Lower Austria. (2) *O. arenarium* Waldst. et Kit. from Hungary, etc. (3) *O. arenarium* auct. gall. an Waldst. et Kit.? from the neighbourhood of Maintz and from S.E. France. (4) *O. vaudense* Gremli from Switzerland. (5) *O. echioides* Gren. et Godr. et auct. gall. = *O. echioides* L. subsp. *fastigiatum* Braun-Bl. from

France. The three synonyms quoted for β in Sp. Pl. are *Anchusa lutea major* C. B. P., *Anchusa tertia* Cam., and *Anchusa lutea* Dalech. Hist. p. 1102. Although *Anchusa flore exalbido* Clus., which had been mentioned in Hort. Cliff., is not repeated in Sp. Pl., it is included in the Bauhin synonym, which to a great extent is based on it. Clusius described his species first in Rar. Stirp. Pann. p. 677, with figure on p. 678 (1583), and then again in Hist. ii. p. 165 (1601), as a biennial plant growing "in monte Badensibus thermis imminente . . . apud Carnuntum . . . Pannoniæ . . . nunc Petronella vocatum, maxima copia, tum plerisque aliis Pannoniæ Austriæque locis." Both the localities Baden and Petronell are in Lower Austria, where *O. Visianii* grows. This habitat, in conjunction with the very pale flowers and the mention that the plant is biennial, seems sufficient to identify Clusius's plant with that species alone. Nevertheless, the Austrian botanists, as well as Jávorka, treat Clusius's name as including *O. arenarium* Waldst. et Kit. also. If they are right, *O. arenarium* too is covered by *echioides* β . Nothing much can be made of *Anchusa tertia*, but the citation of Dalechamp brings in his *Anchusa lutea*, which "nascitur in sabulosis propter Lugdunum, et qua Lugduno itur Valentiam Allobrogum," thus explaining the "habitat in Gallia" of Linnæus and embracing *O. arenarium* auct. gall., which is well known in the valley of the Rhone. The figure of Dalechamp's plant rather suggests *O. echioides* auct. gall., which must also be included for other reasons. Why Linnæus cites Helvetia as well, I have been unable to discover, but that he has done so sweeps in *G. nudense* Gremli, a form hardly distinguishable from French "*arenarium*."

The Linnean herbarium contains no specimen corresponding to *O. Visianii*; none from Austria, but there are two of French origin. No. 6 is labelled "*echioides*" and "*ex Monsp.*" This Montpellier specimen is haplotrichous, and seems to be precisely the *O. echioides* of Grenier and Godron. No. 7, also haplotrichous, has a label in the handwriting of Latourrette as follows: "*Onosma echioides* L. β ; apud nos planta tota lutea; videtur *Simplitum echii* ampliore, radice rubra, flore flavo Tournef.; ad Rhodanum in siccis et ad vias." This is undoubtedly the *arenarium* of French authors = *O. arenarium* Waldst. et Kit. var. *pyramidalatum* Braun-Bl.

These various forms, whether separated specifically or lumped in a comprehensive species, are not entitled to the plain name *O. echioides* L., which must be confined to Columna's plant. What name or names they should collectively or severally bear cannot be discussed in this note, but we may remark that the conflicting statements as to the characters and duration of *O. arenarium* are most confusing. In the Plant. Rar. Hung. *arenarium* is emphatically separated as perennial from the biennial *O. echioides* Jacq. = *O. Visianii* Clem. Jávorka maintains the distinction, partly on that very ground of duration. The Zürich authors, on the contrary, define *O. arenarium* as biennial, treating *O. Visianii* as a mere subspecies (meaning little more than the variety of most authors), but keep *O. echioides* Gren. et Godr. as a

distinct perennial species. The opinions expressed by Boissier, Fl. Or. iv. p. 181, and his identification of *O. Visianii* with *O. setosum* Ledeb., coupled with the remark on p. 182, "*O. echioides* elatius, corolla longior magis exserta," are in flat contradiction both with Jávorka and with the Zürich authors. Then Brand in the latest edition of Koch's 'Synopsis' takes a different line from any of the others. Most botanists have described *arenarium* as haplotrichous; the Zürich authors as almost so; but in many Hungarian examples obscurely stellate tubercles are discoverable on some of the leaves, consequently Jávorka considers this species heterotrichous, placing it in a different section from the very close *O. Visianii*. A pretty kettle of fish!!

Returning to *echioides* L. as the name for an asterotrichous species, it may be admitted that Linnæus, had he possessed sundry asterotrichous *Onosmas* such as true *stellulatum*, *erectum*, etc., would perhaps have lumped them together with Columna's plant and with the above-mentioned specimen no. 5 in a collective *echioides* α , whilst separating the haplotrichous series β . This is the procedure which appeals to the school of which Dr. Briquet is so distinguished an ornament, and which the Zürich authors appear to follow, requiring a collective name for all closely-related asterotrichous species. The objection to the method in this case is that, in the absence of a complete monograph of the genus, it cannot be scientifically carried out without the study of very numerous allied Asiatic forms, which are by no means the same as the European. This study has not been facilitated by the rather reckless determination as *echioides* or as *stellulatum* or *tauricum* of many specimens from Asia Minor to Afghanistan and the western Himalaya. It has certainly not been successful as adopted by Boissier in the 'Flora Orientalis' for the group he collects under the name *stellulatum*, the true *stellulatum* Waldst. et Kit. being a remarkably definite entity with a very limited area, chiefly Croatian. The Zürich authors have preferred the name *tauricum* Willd. for a similar purpose, as being six years earlier than *stellulatum*, ignoring the material differences that exist between true *tauricum*, *stellulatum*, and *echioides* (which they actually call *echioides* Wettst. non L.!!).

We must differ *toto cælo*; if there must be a "species cloaca" it should bear the Linnean name *echioides* and no other, though not in the more precise sense that I have advocated above. The haplotrichous series must be left to find some other generalized appellation.

THE ONOSMAS OF SIBTHORP.

Sir J. E. Smith has made a terrible hash of the *Onosmas* collected by Sibthorp. Five species are mentioned in the 'Prodromus' (1806), of which only three reappear with figures in the 'Flora Græca.' The five are:—

No. 421. *O. orientalis* with no diagnosis or figure; said to grow "in insulæ Cypri campestribus; Sibth. MSS.," with the local name *ἐυλοθρόμβος*

and assumed by Smith to be the *O. orientale* of Linnæus. This is an extremely improbable identification, for *Podonosma syriacum*, which is the Linnean *O. orientale*, is not known from Cyprus. As Sibthorp's herbarium contains no specimen, it is impossible to ascertain what species was intended, unless the identity of *ξυλοθρόμβος* were to be definitely determined by local inquiry in the island.

No. 422. *O. montana*. This is represented by a single example, *sine loco*, in Sibthorp's herbarium. There is a figure of this specimen in Nuov. Giorn. Bot. It. xxxi. tab. 3. It is an exceedingly strigose plant, with stout bristles, borne on stellate tubercles, spreading in every direction, and is identical with sheet no. 5 in Herb. Linn., which has been spoken of above. It might therefore be regarded as *O. echinoides* α Linn. herb., non Sp. Pl., and is certainly not the *O. echinoides* of Smith's tour or the plant known to Columna, but is identical with the very strigose form of *O. pallidum* Boiss. found in the neighbourhood of Smyrna. Sibthorp may have collected it during his stay in that city, or possibly on the Bithynian Olympus, the home of *O. Aucherianum* DC., Prodr. x. p. 60 (1846) = *O. scaberrimum* Boiss. et Heldr. in Pl. Anat. 1846, both of which names were afterwards united by Boissier to his *O. pallidum*, Diagn. ser. 1, xi. p. 112 (1849), as an exceptionally strigose form. Later again, in Fl. Or. iv. p. 201 (1879), he unfortunately annexed *pallidum* as var. β to *O. stellulatum*, uniting under that variety his original Anatolian *pallidum* with European forms from Greece, Macedonia, and Thrace, that are more nearly allied to, if not identical with, *O. viride* (Borbás) Jávorka.

As far as Smith's diagnosis of *O. montanum* goes it would apply to Sibthorp's specimen, as well as to other forms that no one thinks of calling *montanum*; but his unfortunate quotation, as synonymous therewith, of Columna's figure and of Tournefort's *Symphytum echii folio angustiore, flore luteo*, which we have seen to be identical with Columna's plant from the central Apennines, has led to the misapplication by Italian botanists of the name *montana* to their plant. It seems incredible that Smith should have made such a mistake, for in his 'Sketch of a Tour on the Continent,' p. 308 (1793), he tells us: "we came to Valcimiru, 136 miles from Rome . . . At the back of the inn I gathered . . . *Onosma echinoides* Column. Ecphr. 183, which seems to be a distinct species from the Linnean variety β found about Montpellier, being less hairy, and the bristles on the leaves are curiously stellated at their base." Exactly so; and in his herbarium lies the very specimen that he gathered—a splendid example of Columna's plant, but *toto cælo* different from Sibthorp's. We can only suggest that when he was going through Sibthorp's plants he did not take the trouble to compare his own specimen collected many years earlier, or he could hardly have failed to

notice that its resemblance is not to the *montanum*, but to the *erectum* of Sibthorp's herbarium.

What may be the exact relationship of the specimen labelled *montanum* to the sundry Greek forms united by Halácsy, Consp. Fl. Gr. ii. p. 334, under *O. echioides*, as understood by him, and to *O. viride*, is a matter for investigation. The habitat alleged in Fl. Gr. Prodr.—“in insula Creta et in Peloponneso”—cannot be correct. No plant resembling the specimen is known from Crete, and none that I have been able to see from the Peloponnesus agrees with it, nor does Columna's Apennine plant occur in either region, although it is very closely related, not indeed to the *montanum* of the herbarium but to *O. erectum*.

In these circumstances the name *Onosma montanum* must be abandoned as being “a permanent source of confusion or error,” in the language of the International Rules, Art. 51, case 4. It must be rejected altogether.

No. 423. *O. echioides*, synonymized by Smith with *O. echioides* Sp. Pl., is well known not to be any form of the Linnean *echioides*, but it is obviously the haplotrichous *O. frutescens* Lam., as appears from the figure in Fl. Gr. 172 and from Sibthorp's own specimen.

No. 424. *O. erectum*. This well-known Greek species is not so well figured as usual in Fl. Gr. t. 173. The colour is too green, the plant always being very grey in nature, and the drawing of the flowering cyme may have misled Smith into the diagnosis “*floribus erectis*,” which is misleading. The position of the flowers in reality is not more erect than in allied species, such as *echioides* var. *Columna*, but as usual there is a gradual change of position from the nodding bud to the erect fruit, as the scorpioid inflorescence unwinds. The rest of the characters given in the ‘*Prodromus*’ are admirable: “*foliis linearibus, pilis basi stellatis intertextis, caulibus simplicibus erectis*”; these distinguish it perfectly from the herbarium specimen of *montanum*, in which the leaves are oblong and obtuse, the stellate hairs of one tubercle do not overlap those of its neighbours; and the stems are diffuse or ascending, but they would not provide differentiae from the Sicilian form of *echioides*, *O. canescens* Presl. In the ‘*Flora Orientalis*’ Boissier has ignored these characters, identifying *erectum* and *montanum*. I do not think that he ever saw Sibthorp's specimens of either.

Onosma erectum comprises two varieties or subspecies—one with glabrous corollas, peculiar to the mountains of Crete; the other with strongly pubescent flowers, var. *pubiflorum* Hal., plentiful on Hymettus and other hills in Attica; also occurring, according to Halácsy, in Eubœa and Achaia. Crete alone is quoted as the habitat both in the Prodr. and in Fl. Gr. ii. p. 62, but it is obvious from inspection of Sibthorp's specimens that none of them come from that island. There are two sheets in existence, both containing several

pieces *sine loco*. One is at Oxford, the other at Kew; the latter having formed part of the herbarium of R. C. Alexander, who afterwards took the name of Prior. At one time he worked under Dr. Daubeney, the Curator of the Oxford Herbarium, who probably gave him this sheet, with the usual contempt of that date for "mere duplicates." The pieces on this Kew sheet obviously come from Attica, being identical with numerous examples from Hymettus.

The Oxford examples, however, consisting of three pieces on one sheet, are very remarkable. It is equally obvious on comparison that these do not come from any part of Greece, but from Sicily, being exactly *O. canescens* Presl = *O. echioides* var. *crinitum* mihi, a form peculiar to that island and very closely related to Columna's Apennine plant, yet differing from that and from *erectum*, either of Crete or Attica, by its yellow tinge *in sicco*, and in its remarkable shagginess, being clothed with copious spreading bristles, those of the stem exceeding in length its diameter. The corollas are pubescent. Sibthorp did not visit western Sicily, where this *Onosma* frequently occurs and whence come practically all the examples to be seen in herbaria; but he was at Messina, and the Florence herbarium contains one sheet, no. 36, of specimens from Monte Scuderi, half-way between Messina and Taormina, which are absolutely identical with those at Oxford. This should not lead us to think *O. erectum* a *nomen confusum*, for the description, the habitat, the Kew specimens, and above all the figure in 'Flora Græca' completely outweigh the discrepant origin of the Oxford specimens. Whether the monographer of the future will unite *erectum* to *echioides* (Columna) as a subspecies peculiar to Greece is another question.

No. 425. *O. fruticosum*, a very distinct shrubby species from Cyprus, figured in Fl. Gr. t. 174, of which the herbarium contains a specimen. It is strange that Boissier should have overlooked Sibthorp's name, which dates from 1806, the year of pages 1-218 of the 'Prodromus,' in favour of *O. fruticosum* Labill., Syr. Dec. iii. p. 10, which is the same Cyprian plant, but was not published till 1809. Ind. Kew. too, which as usual in such cases copies Boissier, ignores Sibthorp in favour of Labillardière.

Sibthorp's herbarium further contains an unnamed specimen, *sine loco*, differing from any of the above. It is asterotrichous, with oblong, obtuse leaves, not revolute at the margins, scabrous but hardly strigose, with remarkably short calyces and strongly pubescent corollas. It is not in very good condition. As yet I have found no match for it in the herbaria I have been able to consult. It may perhaps be the form called *echioides* var. *brachycalyx* by Halácsy, of which I have not seen an example. The sheet has a label (not Sibley's nor Smith's) attached, reading "Herb. Sibthorp. South of Europe 97."

There is little hope of eliciting more information about Sibthorp's *Onosmas*. Dr. Druce has most kindly allowed me to examine the few scrappy notes and lists that exist at Oxford, with the following scanty result :—

- (1) Among the sheets of pencil sketches of details of plants made by Bauer in the field, there is only one, a very slight one, of an *Onosma*. It bears no name and is on a sheet of drawings made in Asia ; it seems to be part of a plant of the same character as the *montanum* specimen ; at any rate it does not resemble any other species of the 'Prodrömus.'
- (2) The names *montanum* and *erectum* were not given by Sibthorp himself, but by Smith, either because Sibthorp had not named the specimen, or because his naming was obviously wrong. The first reason probably accounts for *montanum* ; *erectum* is certainly due to the second, for in a small undated notebook of Sibthorp's there is the following entry : "*Onosma simplicissima* L. Sp. Pl. 196 ; Icon propria, Ht. in montibus Sphaciæ." Now there is no doubt that tab. 173 does represent the *Sphakia* plant, and Smith, who had Linnæus's specimen of *simplicissima*, must have seen that it could not be that species. From Smith's label on specimen 424, he seems to have taken it at first for *O. sericeum* Willd. and then altered the label to his own new name *erectum*.
- (3) In the same notebook there is another entry : "*Onosma orientalis* L. Sp. Pl. 196 ; Icon propria. Ht. in campis prope Byzantium." This, of course, is the species figured in tab. 172 (really *O. frutescens*), which Smith rightfully considered not to be *orientalis* L. and quite wrongly determined as *echioides*, a determination which would surely have been impossible for Sibthorp himself, who had labelled *echioides* two specimens, nos. 808 and 809, in Herb. Sherard at Oxford. Both are *sine loco*, but obviously 808 is *echioides* var. *Columnnæ* and 809 is *helveticum* Boiss.

The long years through which the preparation of the 'Flora Græca' dragged led to the rest of Sibthorp's papers, including his journals, passing from hand to hand ; their ultimate fate is a mystery. It is to be hoped that Dr. Druce will some day give a complete account of all the incidents connected with the publication of the great work.



This is a photograph (natural size) received from Dr H O Juel, of the specimen in Hasselquist's collection at Upsala which Dr Juel has identified with *Onosma orientale* Linn. The sheet has nothing written on it except the letters "aeg". The specimen is obviously the Syrian *Podonosma syriacum* Boiss, not the Egyptian *P. galatense* Schweinf --
C C LACINA, 13 VII 1923

On the Function of the Bladders in *Utricularia vulgaris* L. By C. L. WITHEYCOMBE, Ph.D., D.I.C. (Communicated by J. RAMSBOTTOM, O.B.E., Sec.L.S.)

(With 11 Text-figures.)

[Read 29th November, 1923.]

IN 1916 (8) I published a short note on the function of the bladders of *Utricularia*, showing that these were not passive traps, as was generally considered to be the case, but that they captured prey by active movement in response to stimulus. A bladder became sensitive to contact after its walls had become concave on each side. Then, on touching certain short hairs at the mouth of the bladder, the lateral walls sprang outwards, becoming somewhat convex and so drawing a current of water into the bladder, which swept with it, of course, any body sufficiently light to be sucked in.

These observations were made under some difficulties, and a hand-lens was my only aid to vision. Thus I would excuse a certain crudeness and inaccuracy of detail in this paper. As soon as a fresh opportunity offered, observations were recommenced and material was obtained for a more complete paper, with the intention of publishing a full account of the mode of action of the bladders, from the results of a number of experiments.

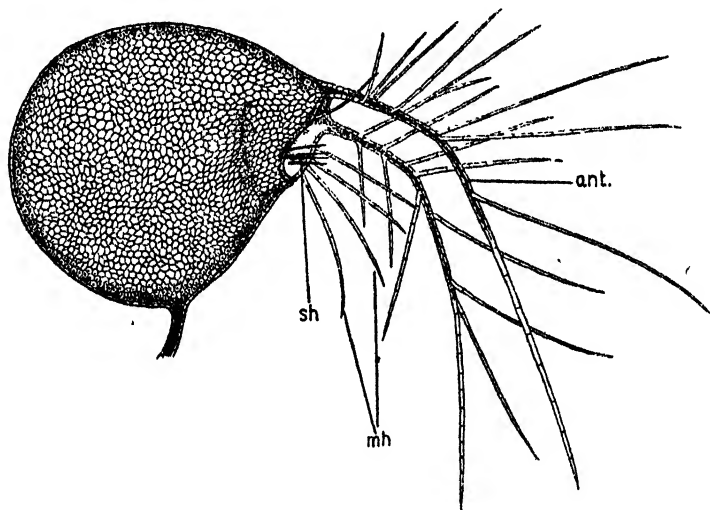
In 1922, however, a paper by Merl (6) appeared, and Mr. J. Ramsbottom kindly drew my attention to this when the writing of my projected paper had already been commenced. From Merl's account I learned that Brocher (2) had published a paper in the 'Annales de Biologie lacustre' in 1911, and had essentially discovered the mode of action of the *Utricularia* bladder, so that to him belongs the credit for first discovering the true nature of the bladders. Brocher (2) put forward a theory to explain the mechanism of the bladder, and suggested that, when sensitive, a negative pressure obtained within. In this sensitive condition the valve closing the mouth of the bladder bulged convexly outwards and fitted the orifice to make it quite watertight. On stimulus he suggested that the valve straightened itself, ceasing to remain convex, so that it no longer fitted the mouth of the bladder so completely. An influx of water immediately occurred, carrying with it any victim near at hand.

With Brocher's suggestions I found my own observations mainly in agreement—that is to say, his theory of negative pressure seemed to be borne out by my own experiments; but I do not think that his interpretation of the valve action is correct. This is certainly difficult to observe, and Brocher himself says that he only puts forward his suggestion as a tentative hypothesis.

Merl (6) made a large number of experiments upon the bladders, and many of his results are very similar to my own. It would therefore now appear superfluous to give all mine in full, and only such will be mentioned as bear upon the mechanism of the bladder. For the effects of varying conditions, reference should be made to Merl's paper.

Two theories for the mode of action of the bladder were put forward by Merl. Both appear to me to be rather indefinitely stated, and I am not sure that I have followed his meaning exactly. On page 72, in summing up the action of the bladder, he says: "Sicher unrichtig ist, sie mit Wachstumserscheinungen oder den Druckverhältnissen der darüber lastenden Wasser bzw. Luftmasse in Zusammenhang zu bringen." This statement, or rather the latter part of it, seems to me to preclude Brocher's "negative pressure"

FIG. 1.

Bladder of *Utricularia*. $\times 50$.

theory, with which latter I would agree in principle. As alternatives Merl suggests, first, that the bladders exhibit irritability similar to that seen in *Aldrovanda* and *Dionæa*; apparently he considers the walls to bulge forcibly outwards on stimulation, as do the leaf-lobes of *Dionæa* inwards. Secondly, Merl says that the only possible alternative theory is that the walls are pulled together by cohesion of water, and that there is a labile equilibrium between the pressure of the elastic valve and the pull of the walls. He seems to regard this last theory as the more improbable, and says, on the contrary, that bladders containing bubbles of air can still act in response to stimulus. He adds that automatic "firing" would probably occur with such a mechanism when the pull within had become too great for the valve to withstand. He was not

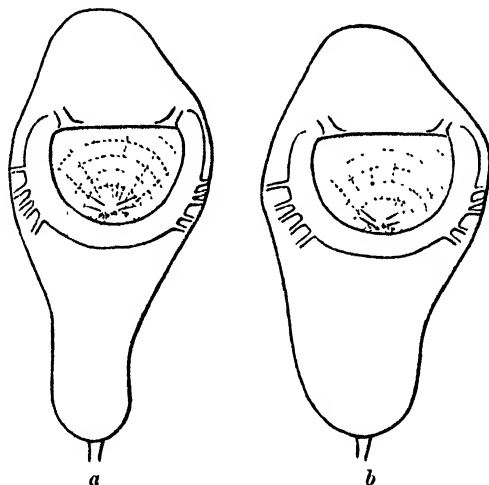
able to test bladders with suspensions in water, as they were too sensitive to permit of examination under a high power.

Admitting, then, the evidence of the majority of Merl's experiments, but differing from his arguments, I will now proceed to outline my own observations and deductions therefrom.

DESCRIPTION OF BLADDER.

First, to give a brief account of the bladder. It is somewhat oval in shape, flattened laterally, and attached by a short footstalk to an appendage of the plant (fig. 1). Whether the bladder represents a leaf does not concern us in the present discussion. The wall of the bladder is thin, usually being but two cells in thickness (fig. 4). The cavity is lined within with numerous quadrifid absorptive hairs (fig. 3, *e*).

FIG. 2.



Walls of the bladder. $\times 50$.

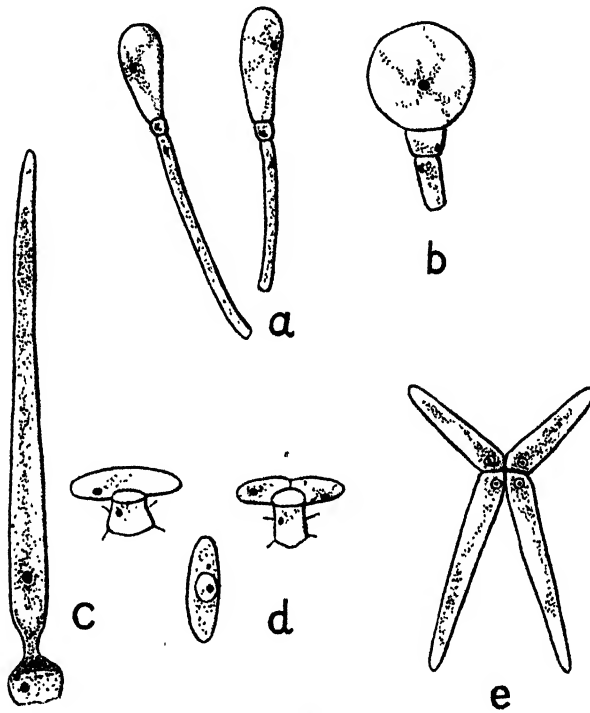
To facilitate description, the attached part of the bladder will be referred to as ventral, and the opposite, of course, as dorsal. The opening of the bladder will be termed anterior.

The mouth of the bladder is somewhat circular, flattened dorsally. Ventrally, in a semicircle a thickened collar ensures rigidity of the rim of the orifice. From the dorsal part of the rim hangs down a flap, which will be referred to as the valve. Both terms are those previously used by Darwin (5) and seem well adapted to the structures in question.

The collar is a semicircular pad of large parenchymatous cells (fig. 5, *co*). Covering this and actually forming a sharply differentiated zone round the inside and lower half of the mouth is a triple layer of highly-specialized cells (fig. 5, *ul*, *ml*, *be*). In surface view these cells are seen to be thicker-walled

and elongate oval in shape ; their length lies in the same direction as that of the collar. The cells are not fused with each other, but are in close proximity. In longitudinal section of the bladder (fig. 2) it is seen that uppermost is a layer of apparently columnar cells (fig. 5, *ul*), the cells having been cut across their width. Below this is a thin middle layer of smaller cells (fig. 5, *ml*). Again, below the middle layer is a basement layer of cells (fig. 5, *be*), rather similar to the upper layer and continuous with the epidermis of the bladder. Projecting into the bladder cavity from the posterior (interior) margin of the collar are some elongate hairs (fig. 3, *e* and fig. 5, *eh*), and on the extreme

FIG. 3.

Different types of hairs. $\times 400$.

margin of the collar are several club-shaped hairs (fig. 3, *a* and fig. 5, *ch*) similar to those on the rest of the rim and on the valve. All these hairs are doubtless homologous with the quadrifid absorptive hairs lining the bladder cavity.

The valve or flap (*v*) closing the bladder mouth is a continuation of the dorsal wall of the bladder (fig. 4). It is two cells in thickness, and is of such shape as to close the mouth completely when its ventral, free margin is applied to the collar. The valve consists of three ill-defined regions. An upper, dorsal region with both layers of cells composing it fairly similar.

This region presents a slight concavity when viewed from outside. From this concavity, mainly at the sides, arise numerous club-shaped glandular hairs (fig. 3, *a*). These are each composed of three cells: (1) an attaching stalk cell, more or less elongated; (2) a short (square in section) middle cell; and (3) a swollen distal cell forming the club. Similar hairs to this occur round the rim, but they are most common dorsally. The middle region of the valve bulges slightly outwards from the bladder normally. The cells of the outer layer of this region are similar to the special cells of the next region in that their walls have some ridges projecting internally, mainly at the angles of the cells. The inner layer is composed of larger, thin-walled cells, which from their structure would readily allow an inward flexion of the valve (fig. 5).

Marking the commencement of the third and marginal region of the valvular flap are four bicellular hairs (*sh*). These are quite simple tapering hairs, the basal cells of each being an outgrowth of one of the epidermal cells of the valve. The distal portion tapers gradually to a point. These hairs are the only sensory hairs and upon stimulus cause the bladder to respond. Situated near the sensory hairs are three or four peculiar club-shaped hairs, which are not noticeable from the fact that the terminal cell of each is larger than usual and is almost spherical (fig. 3, *b*). Other club-shaped hairs occur near by, but more exteriorly, and these are not so large or spherical distally.

From the region enclosed by the four sensory hairs, and appearing to radiate outwards to the free margin of the valve, are specialized cells which I consider as the principal motor tissue (fig. 6, *mt*). These cells are slightly thicker-walled than other cells of the valve, and they have many projecting ridges from their walls internally. Other cells of the valve belonging to the middle region, as already seen, show similar thickenings, but by no means to such an extent as in the present region.

The free edge of the valve fits into a slight groove along the anterior margin of the zone of specialized collar cells (fig. 5, *g*). This groove is as deep as the middle layer (fig. 5, *ml*) of the collar zone. After action the valve always springs back, and its edge is held in this slight groove. A certain amount of mucus is secreted (fig. 5, *m*) apparently by the middle layer, and this makes complete a watertight fitting of the valve. The mucus is easily demonstrated in sections if the bladders have been fixed in Bouin's Picro-formol. In the process of imbedding and staining, all picric acid is washed out, but the mucus above-mentioned retains a conspicuous yellow or orange colour to the last, and is well seen in a preparation stained with hæmatoxylin. It is seen to extend also for some distance along the middle layer of cells.

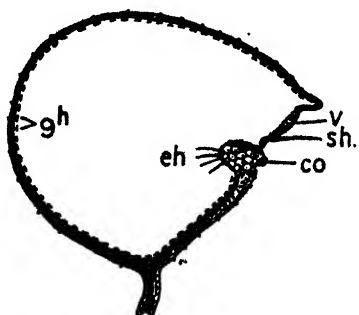
From the two dorsal "corners" of the rim arise long, branched, antenna-like processes (fig. 1, *ant.*). These plumose antennæ bend downwards and outwards. Laterally, from each side of the rim are about five simple

multicellular hairs (*mh*). All the hairs from the rim spread out funnel-like, so as to lead intruding animals direct to the bladder mouth. Also distributed round the rim are a number of club-shaped hairs (fig. 3, *a*). Scattered over the outside of the bladder wall are small, rounded, sessile glands (fig. 5, *sg*) homologous with club-shaped hairs.

MECHANISM OF BLADDER.

After "firing," the lateral walls of the bladder are slightly convex (fig. 2, *a*). The free margin of the valve has sprung back to its position, fitting into the groove in the zone of specialized collar cells (fig. 4). A slight amount of mucus is secreted, and the bladder is sealed hermetically. The quadrifid hairs lining the bladder constantly absorb the fluid within, whether this fluid is pure water or an infusion of decaying animals. With reduction in volume of contained water the bladder must yield to external pressure; therefore the lateral walls bulge inwards, presenting a concavity externally on each

FIG. 4.



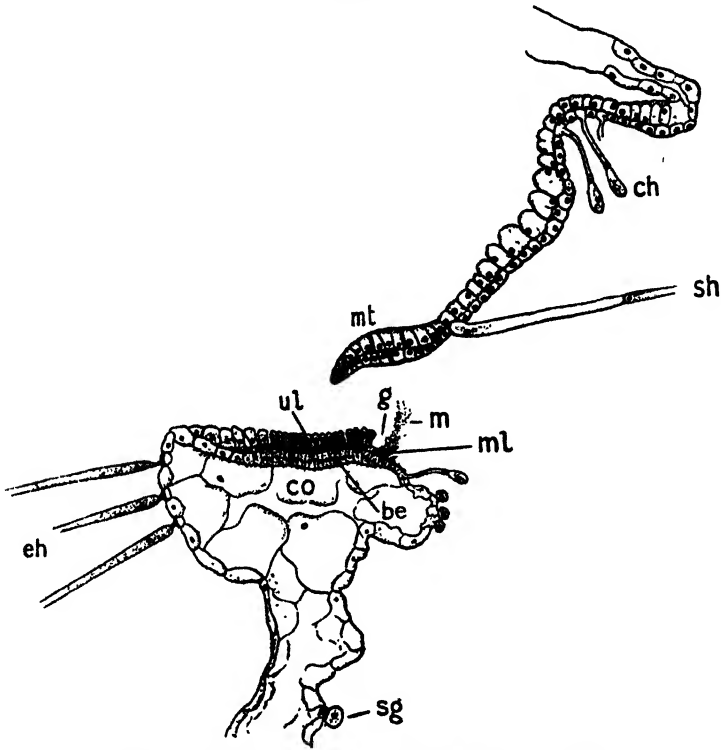
Section of bladder, enlarged. $\times 50$.

side (fig. 2, *b*). They, however, exert some tension, and would, on release, spring back to their former position. The quadrifid hairs continue to absorb until equilibrium is reached between the internal negative pressure and the osmotic tension, which can be exerted by the cell contents of the quadrifid hairs. We have now a considerable tension upon the valve, tending to pull it inwards; but this cannot happen, since the cushion of specialized collar cells prevent the free margin of the valve from moving inwards. The valve is also so constructed that it continues to bulge exteriorly at its centre, this condition being mechanically more stable than if the valve were plane or concave. Were the latter actually the case the valve might easily be sucked inwards, its edge slipping over the special cushion of collar cells.

There is only one movement which can possibly release the valve from its catch. This is an upward movement. Such seems to occur when either of the four sensory hairs are touched. Once an upward movement has removed the free edge of the valve from its groove (fig. 5), the negative pressure

within the bladder causes an influx of water. The influx being completed, the valve once more springs back to its former position. Such appears to be the mechanism, as far as my observations go. Brocher suggested a straightening of the valve instead of an upward movement. He did not observe that the valve margin was retained in any particular way, but thought that it was merely closely adpressed to the collar.

FIG. 5.

Section of opening of bladder, enlarged. $\times 200$.

REASONS FOR FOREGOING THEORY OF MECHANISM.

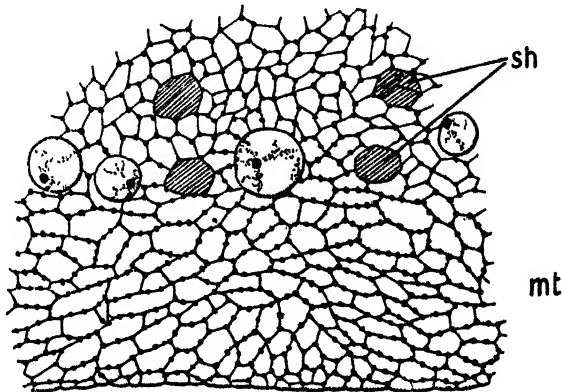
It has been suggested that absorption of internal water is carried on by the quadrifid hairs lining the bladder. These seem to be the most likely agents. Previous investigators came to the conclusion that these hairs were absorptive, and, indeed, there seems to be no reason for doubt. They certainly absorb methylene blue very rapidly, and that they are probably homologous with the mushroom-shaped glandular hairs of *Pinguicula* adds weight to the suggestion of their absorptive nature.

That there is a negative pressure within the bladder seems to me to be proved by the fact that if a concave (sensitive) bladder is pierced with a needle, the walls immediately spring outwards and back to their convex

(insensitive) condition. That the pricking is not sufficient stimulus to "fire" the bladder is shown by the fact that the bladder may be pricked superficially in any part, or even severed from its footstalk without "firing," or the bladder may often be actually penetrated by the needle; if the latter remains filling the puncture and no water enters from outside, the bladder remains concave. It is when water is allowed to enter through the puncture that the walls spring outwards.

Merl (6) states that there can be no negative pressure, since bubbles often occur in bladders and such bladders still act. It would seem more correct to say that bladders act, but to a feebler extent when containing air, and also that if a bladder encloses a large bubble, it does not act. It is true that one would expect a bubble to increase in size with decrease in pressure, and this does not appear to occur to any noticeable extent, although some quite definite increases have been observed. Probably the reason why no very appreciable

FIG. 6.

Motor tissue. $\times 400$.

increase in size can be detected is that the bubble moves its position as the walls decrease the bladder cavity posteriorly, and that it moves to a position where the cavity is broader. Assuming that the pressure within a sensitive bladder is half that within a recently "fired" bladder, then a bubble would only increase to double its volume. Such an increase would be approximately the amount which seems to occur, and it is, of course, not very noticeable when allowed for in three dimensions. The suction of a bladder containing air is never as great as that of one which contains only water, and the larger the bubble contained, the less the suction, a large bubble causing a bladder to function entirely. It should be noted that it is not normal for bladders to contain any gas. Plants grown from winter buds and continuously in water have bladders without air. When plants are removed from water, the sensory hairs are stimulated and air enters the bladders. This occurrence is denoted by a popping sound as the plants are removed.

THE VALVE.

It has been shown that Brocher's theory of valve action cannot be accepted, as the valve can only be released by an upward movement from its groove (fig. 5, *g*) in the collar zone.

Merl's theory of a labile equilibrium between valve and tension within bladder can also not be accepted, as the pressure required to force open the valve of a sensitive bladder is relatively considerable. On the other hand, the slightest touch of the sensory hairs causes immediate response. Merl states that he found the bladders too sensitive for observation under high powers. This I have not experienced. As long as the sensory hairs are not touched there is no response.

The following method for observation of the valve was generally successful. A sensitive (concave) bladder was selected upon a plant, its footstalk was severed, and while still under water it was floated into a small salt-spoon. This was then lifted out full of water, and transferred to an excavated glass block containing water. The bladder was then adjusted to stand with valve uppermost between supports, and the water contained in the excavated glass block was pipetted off to a convenient level, but not low enough to bring the sensory hairs into contact with the surface film of water.

For testing the valve a piece of human hair was inserted into a handle and cut off short, allowing about one-eighth of an inch free. This short and comparatively stout piece of hair was then pushed against various parts of the valve, using for observation a Watson Greenough dissecting binocular with 27 mm. objectives and oculars number 3 or 6. It was found that the valve would nowhere yield to pressure except at the lower margin of the valve, where pressure frequently caused the hair to slip into the bladder between the collar and the valve, thus of course "firing" the bladder. Rough friction or pressure of the club-shaped hairs covering the valve and rim produced not the slightest response. The only hairs sensitive to stimulus were the four tapering sensory hairs on the valve.

The valve is so sprung that it always returns to its position with some force, even after being pushed open ventrally several times. The shortest time of recovery of sensitivity that I have observed is thirty minutes, and this I considered a distinct record. Merl gives fifteen minutes as the shortest time. Recovery is retarded by low temperature, but other factors are also involved, and in my own experiments a regular time-temperature relation has not been obtained.

As regards the nature of objects touching the sensory hairs to cause response, these must be either solid bodies or the like. Contact with the surface film of water is often sufficient to "fire" a bladder. Some liquids will also irritate the sensory hairs, but such appear to be injurious. Bouin's Picro-formol, used as fixative, can be added to a watch-glass containing sensitive bladders in water without causing these to "fire," and by very

gradual steps, bladders can even be imbedded in wax for sectioning while still in the concave condition. The bladders do not allow of penetration by fixatives very rapidly, and the usual time of immersion in Bouin's Picro-formol (full strength) was twelve to eighteen hours. Several cases have been encountered of bladders responding to rough stimulus of the valve after having been in the above fixative for half-an-hour. I cannot believe that these were still living. •

If stains are added to the water in which plants are growing, these do not enter the bladders for a considerable period. Even methylene blue, which is such a useful *intra vitam* stain, does not enter for a day or two, and if then, it is probably due to death or injury of the bladder. Such facts as these would appear to prove conclusively that the sealing of the bladder is very perfect.

The mode of action of the bladder may therefore be summarized as follows. The bladder is hermetically sealed by the springing back of the valve into a groove, and the sealing is rendered more complete by the secretion of mucus by certain of the collar zone cells. Water is absorbed from within the bladder, probably by the quadrifid hairs. This produces a negative pressure within, so that the lateral walls are drawn inwards, often so near as almost to touch each other. They tend always to spring back to the previous slightly convex position, and no doubt therefore exert a pull. When either of the four sensory hairs upon the valve is touched, certain motor tissue, mainly ventrally to these hairs, contracts, thus withdrawing the valve margin from its groove and allowing an opening of the valve with its consequent influx of water. The valve immediately springs forward to its former position, fitting into the collar zone.

No part of the bladder is sensitive to touching except the four sensory hairs upon the valves. Other hairs, whatever their form, are insensitive.

As regards the nature of prey captured by *Utricularia*, various records appear of small crustacea, insect larvæ, worms, etc. Moseley (7) mentions that Mr. G. E. Simms had observed numbers of young fish caught in the bladders by head or tail or even by the yolk-sac. I have seen a tadpole (8) held firmly with the head in one bladder and the tail in another. Also small molluscs (*Planorbis lineatus*) and a colonial Polyzoan (*Cristatella mucedo*) have been observed held at the mouth of a bladder.

Whether the animals caught are digested, as in *Pinguicula*, or whether they merely decay, is still somewhat of an open question. The chemical secretions of the bladders have been fully investigated by von Luetzelburg (5), who brings forward much evidence in favour of true digestion.

TECHNIQUE.

It may be useful to add a note on the method of imbedding bladders for sectioning with as little alteration in form as possible. The following gave best results.

Bladders in sensitive condition were severed from the plant under water by cutting through their footstalks. The bladders were then carefully floated into a small spoon, taking care throughout not to touch the sensory hairs. The spoon, full of water containing bladders, was then removed and immersed in Bouin's Picro-formol, contained in a suitable vessel. The bladders were now floated out into the fixative and the spoon removed. After some minutes and mixing of the water from the spoon with fixative, a large part of the diluted fixative was removed and fresh added in the place of it, so that the strength was nearly normal undiluted. Fixation was allowed to take place for from twelve to eighteen hours to make sure of penetration, though probably much less would have sufficed. After the above period the Picro-formol was removed and replaced by 50 per cent. alcohol, the operation being carried out with due care, keeping the bladders always immersed in fluid. The 50 per cent. alcohol was next replaced by 70 per cent. after an hour or so, and all picric acid was washed out in 70 per cent. alcohol. By similar gradual replacement the bladders were carried through 90 per cent. to absolute alcohol, and then by the method of flotation, with removal of surface-layers from time to time, into a mixture of equal parts chloroform and carbon-bisulphide. When at last in the pure mixture of chloroform and carbon-bisulphide, chips of paraffin-wax of about 40° C. melting-point were added and dissolved. The solution of wax when saturated was placed in an open vessel on the top of an imbedding oven, outside, in order to drive off much of the chloroform and carbon-bisulphide. At last the bladders were left in almost pure wax, and were then placed in a bath of wax 52° C. to 56° C. melting-point within the oven. Two changes were given over a period of four to five hours. Sections were cut on a Jung-Thoma microtome, and finally stained with Heidenhain's Iron Hæmatoxylin, or Delafield's Hæmatoxylin counterstained with Biebrich Scarlet.

In conclusion, I would express my indebtedness and sincere thanks to Mr. J. Ramsbottom for his kindness in communicating this paper, and to the Staff of the Botany Department, British Museum (Nat. Hist.), for affording me every facility and help in referring to literature.

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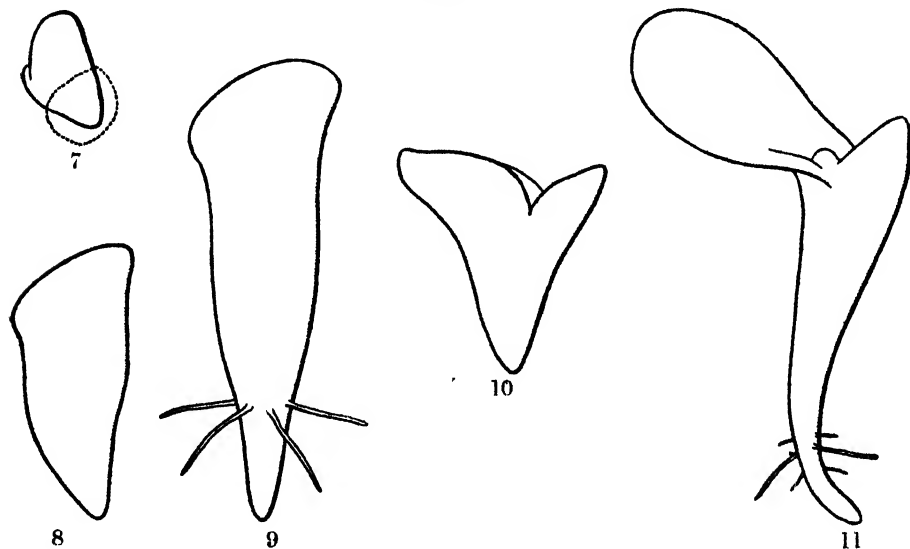
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NOTE ON THE POST-EMBRYONAL DEVELOPMENT OF *UTRICULARIA VULGARIS* L.

In 1877 (4) F. Kamiński published a full account of the development of *Utricularia*, and this account has been freely quoted from. Kamiński's figure of a germinating seed showing its cluster or whorl of filiform leaves arising direct from the seed coat is well known, and, among other books, it reappears in Mrs. Arber's 'Water Plants.'

Some years ago I grew about two dozen *Utricularia vulgaris* plants from seed, and in no case could I confirm Kamiński's account of the post-embryonal development. The seed does not give so directly a whorl of leaves such as he figures, but the development passes through a stage very similar to that of *Pinguicula*.

FIGS. 7-11.

Germination and later stages of *Utricularia*.

After flowering, the flower stems of the plant die and fall into the water. The seeds having ripened, the seed capsule rots, or more often appears to dehisce by the swelling of the seeds within. However this may be, the seeds are as a rule set free at some time during autumn or winter, but they do not germinate.

In the following spring germination takes place, but it is difficult to observe the exact time. Seeds ripened in 1920 germinated from the 26th of March, 1921, to the 2nd of April, 1921. The seed coat ruptures and a fleshy green mass appears from within. This grows to the form seen in fig. 7, although it frequently loses the seed coat before this time. Figs. 8 and 10 show forms seen on the 8th of April, 1921. They may be described as green,

fleshy, and somewhat trumpet-shaped. The radicle is little developed, and no root-hairs are visible at this stage.

Plants seen on the 30th of April are figured at 9 and 11. Both show distinct, colourless root-hairs arising from the radicle. 9 is an unusual form, apparently. 11 conforms with the majority, though all intermediates occur between 9 and 11. It will be seen that 11 has a distinct first leaf, and generally it is extremely similar to a seedling *Pinguicula*. In *Pinguicula*, however, I have been able to observe no root-hairs at so early a stage as this. Scattered over the greater part of the surface of the young *Utricularia* plant are sessile or partially stalked glands, similar to the glands which occur on the outside wall of the *Utricularia* bladder. A most striking fact is that stomata are present only on the upper side of the first leaf, and if a plant is raised to the surface of the water, the stomata are at once thrown off by the apparently waxy upper side of the leaf. Thus the plant floats. Probably in nature few plants float in this way unless accidentally raised to the surface of the water, and plants left submerged develop quite well.

The seedling now grows direct into a typical *Utricularia*. The radicle ceases growth. The second leaf is filiform, and then two or three more filiform leaves may arise. A short stem grows out with another whorl of leaves and generally with a bladder or two. Growth continues to a normal plant, but in the first year little more than two whorls of leaves are produced before the plant forms a terminal winter bud and hibernates.

The present note is offered to point out an existing erroneous idea, or at least one which I have been unable to confirm. Other interesting facts have been observed, and when these have been supplemented it is hoped to publish a full account, but such may be delayed. The development of *Utricularia* is of great phylogenetic significance, and it is hoped that other botanists will repeat the observations briefly stated now.

The Influence of Earthworms on Soil Reaction and the Stratification of Undisturbed Soils. By E. J. SALISBURY, D.Sc., F.L.S. (Reader in Ecology, University of London, University College).

(With 3 Text-figures.)

[Read 15th November, 1923.]

To appreciate the significance of Earthworm action on the acidity of undisturbed soils, it is essential to recognize the marked gradient with respect to hydrogen-ion concentration which such soils exhibit. The author has already shown that just as there is a fairly rapid increase in the organic content of the soil when we pass from the subsoil to the surface, so too there is usually a marked rise in the real acidity in the same direction (*cf.* Salisbury, E. J., "Stratification and Hydrogen-ion Concentration of the Soil in relation to Leaching and Plant-succession, with special reference to Woodlands," *Journal of Ecology*, vol. ix. pp. 220-240, 1922; *cf.* also Discussion on Soil Problems, *Trans. Faraday Society*, 1921). The following data for various types of plant community illustrate this gradient of reaction and organic content in undisturbed soils:—

TABLE I.

Organic Content and pH at Varying Depths.

(Organic $\frac{1}{2}$ Loss on ignition corrected for CO₂ evolved from carbonates.)

Depth in inches.	Oak Wood.	Beech Wood.	Chalk Down.	Pine Wood (nr. Wimborne).
0-2	Org- 17.5% pH 5.4 anic.	Org- 13.0% pH 6.2 anic.	36.0% pH 7.4	Org- 74% pH 4.5 anic.
2-4	" 9.8% pH 5.5	" 9.0% pH 6.0	23.5% pH 7.5	" 74% pH 4.5
4-6	" 7.2% pH 5.6	" 8.8% pH 6.4	23.5% pH 7.6	" 15% pH 4.5
6-9	" 6.1% pH 5.6	" 9.0% pH 7.2	pH 7.6	" 6.2% pH 5.0

Evidence has been adduced elsewhere to show that for a given mineral substratum and with a uniform vegetation there is, up to a point determined by the origin of the organic material, an increase of acidity accompanying increase in the organic content of the soil (*cf.* Salisbury, *loc. cit.*, and Salisbury, E. J., "The Soils of Blakeney Point: A Study in Edaphic Succession," *Ann. Bot.* vol. xxxvi. pp. 391-432, 1922). This, however, only holds where the conditions are approximately uniform, since the rate of decay influences reaction by reason of the earlier stages being more acid than the later stages of decomposition.

The action of the plough in arable land naturally tends to obscure, although it does not completely destroy, the soil gradient, and earthworms in a minor degree perform for uncultivated soils the same function.

It is now over forty years since Darwin called attention to the importance of earthworms affecting a natural cultivation of the soil (*cf.* C. Darwin, 'Vegetable Mould and Earthworms,' London, 1881). He found from observations in four separate locations that the amount of soil brought to the surface as wormcasts ranged in weight from 7.56 tons to 18.12 tons per acre per year. These results were based on continuous collection of the wormcasts from definite areas, and are open to the objection that removal may have stimulated a more than normal deposition at the surface. There is at all events some reason to believe that the wormcast on the surface serves as a protection to the orifice of the worm burrow. The values which Darwin obtained, however, represent an even layer of soil of from .09 in. to about 0.10 in. depth per acre per year, which is considerably less than the corresponding value deduced by Darwin from the depth of burial of objects after a period of years (0.19–0.83 in. per ann.).

During adverse seasons, namely the cold of winter and the heat of summer, earthworms have been known to descend to a depth of as much as eight feet, though they are not usually met with below three feet. The cultivating action thus mainly affects the upper layers of the soil, and in natural soils it would seem that worms feed mainly quite close to the surface. In the great majority of instances where the writer has dug up worms in woodlands, chalk downs, and heaths, they have been found feeding within the top few inches.

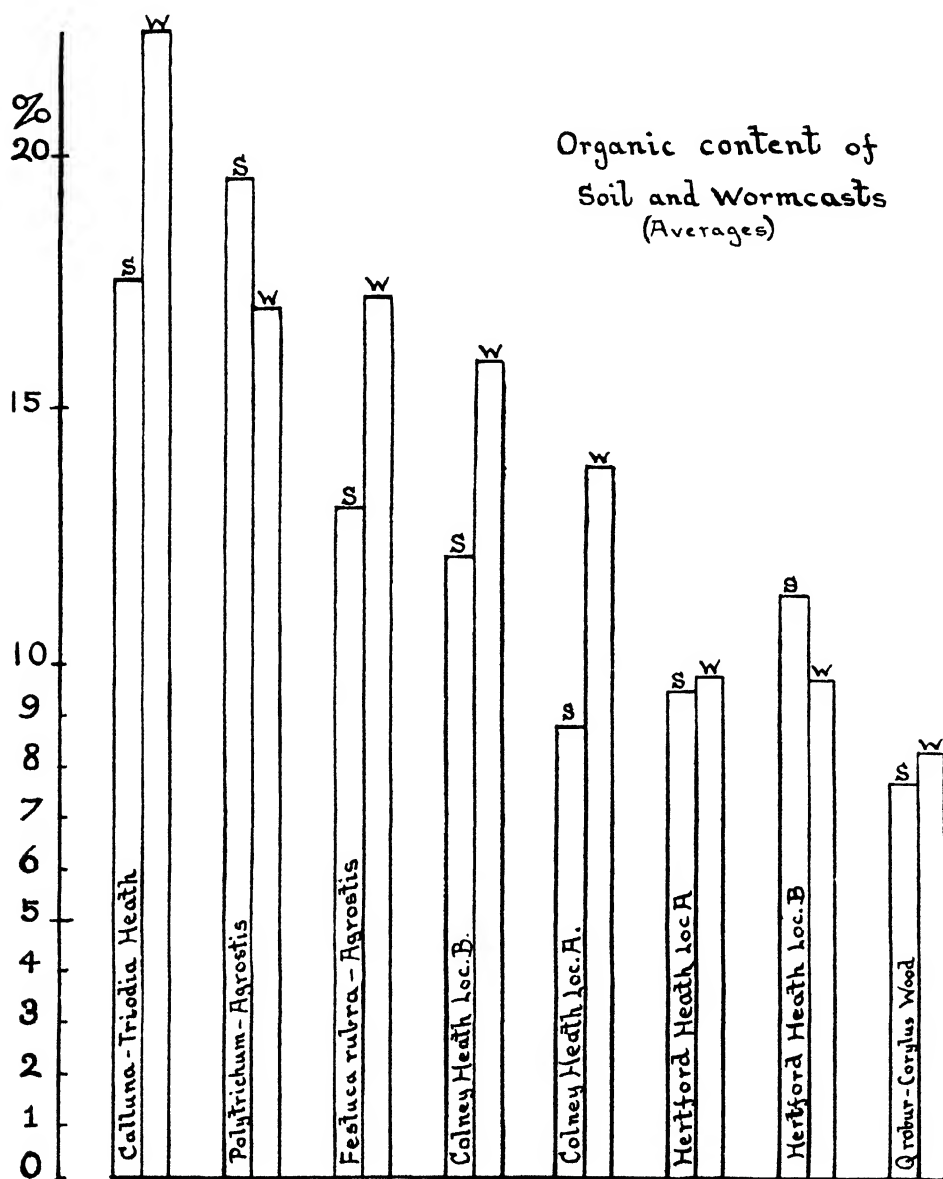
In view of what has already been said with regard to the reaction gradient in undisturbed soils, it is important to know whence the soil is derived which passes through the worm and is deposited at the surface. If the wormcasts show a different reaction to the underlying surface soil, the question at once arises as to whether the wormcasts represent soil from the more alkaline (or less acid) layers of the subsurface or subsoil transported from below, or are they derived from the regions of maximum acidity near the surface?

The obvious test to employ for this purpose is the organic content which, as we have seen, diminishes with increasing depth. Some of the organic material is doubtless decomposed in the passage of the soil through the digestive tract; but if it can be shown that the organic content of wormcasts is higher than that of the subsurface, then any change of reaction as compared with that of the surface must clearly be attributed to direct action of the Earthworm, and not to mere transport of soil from a stratum having a different reaction in the sense observed.

The appended data (Table II. & fig. 1), which represent losses on ignition, corrected for the carbon dioxide evolved from the carbonates, show clearly that in the eight locations investigated the wormcasts were derived from surface soil. The average values for the organic content of wormcasts in

six of the locations are higher, and in three considerably so, than those of the surface soil (0-2 in.). In the two locations where the reverse was the

FIG. 1.



case the difference is not so marked. It would appear, then, that earthworms feed chiefly very near the surface, or, if in the subsurface, in regions of high organic content.

TABLE II.
Average Organic Content (=Corrected Loss on Ignition) of Soils
and Wormcasts.

Location.	Organic Content of Soil (0-2 in.).	Organic Content of Wormcasts.	Difference W-S.
<i>Festuca-Agrostis</i> . Society	13.13 per cent.	17.24 per cent.	+4.11
<i>Polytrichum-Agrostis</i> . "	19.50 " "	17.03 " "	-2.53
<i>Calluna-Triodia</i> . "	17.55 " "	22.45 " "	+4.90
Colney Heath. Loc. A	8.82 " "	13.90 " "	+5.08
" " Loc. B	12.17 " "	15.98 " "	+3.81
Hertford Heath. Loc. A	9.51 " "	9.80 " "	+0.29
" " Loc. B	11.42 " "	9.72 " "	-1.70
<i>Quercus Robur-Corylus</i> . Wood	7.70 " "	8.30 " "	+0.60

TABLE III.
Effect of Earthworms on the Hydrogen-Ion Concentration
of the Soil.

Locality.	Vegetation.	Av. pH of Soil.	Av. pH of Worm- casts.	Differ- ence W-S.
Harpenden.	<i>Festuca-Agrostis</i> (Loc. A)	5.1	5.7	+0.6
"	<i>Calluna-Triodia</i>	5.1	5.4	+0.3
Radlett.	<i>Quercus Robur-Corylus</i>	5.2	5.6	+0.4
Harpenden.	<i>Festuca-Agrostis</i> (Loc. B)	5.27	5.84	+0.57
Radlett.	<i>Q. Robur-Corylus</i>	5.6	6.35	+0.75
Colney Heath.	Nardetum	5.7	6.4	+0.7
Harpenden.	<i>Polytrichum-Agrostis</i> (Loc. B) ..	5.73	5.93	+0.2
Surrey.	<i>Q. sessiliflora</i>	5.8	6.25	+0.45
Colney Heath.	Pasture	6.0	6.3	+0.3
Hertford Heath.	"	6.2	6.4	+0.2
Holmwood Common.	"	6.2	6.43	+0.23
Harpenden.	<i>Polytrichum-Agrostis</i> (Loc. A) ..	6.3	6.7	+0.4
Radlett.	<i>Q. Robur-Corylus</i>	6.5	6.8	+0.3
Markyate.	Scrub	6.9	6.85	-0.05
Radlett.	<i>Q. Robur-Corylus</i>	6.9	6.8	-0.1
Harpenden.	Chalk pasture	7.24	7.27	+0.03
Munden.	Alluvial meadow	7.45	7.33	-0.12
Burton's Down, Surrey.	Chalk pasture	7.45	7.35	-0.1

Range of pH of Soils pH 5.1-pH 7.45.
Range of pH of Wormcasts pH 5.4-pH 7.35.
Range of difference - 0.12 to + 0.75.

Hence any difference of reaction between surface soil and wormcasts may safely be attributed to earthworm action. The data respecting the hydrogen-ion concentration given in Table III. and fig. 2 show that in the majority of localities the wormcasts exhibit a marked reduction in acidity (increased pH) as compared with the soils from which they are derived.

The detailed determinations need not be given in extenso, but two examples, the one from an acid location, the other from an alkaline, will suffice to show the kind of range to be expected in a given area, the soil samples in all cases being taken from the actual level at which the worms were found feeding.

TABLE IV.

Details of Reaction in Two Locations.

A. Acid Soil with *Festuca rubra* dominant and *Agrostis canina*.

pH Values.	No. of Soil Samples.	No. of Wormcast Samples.
5.1	1	
5.2	6	
5.3	1	
5.4	0	
5.5	1	
5.6	1	3
5.7	—	3
5.8	—	—
5.9	—	2
6.0	—	2
6.1	—	2
6.2	—	1
Total Samples	10 (Av. pH 5.27).	13 (Av. pH 5.84).

B. Alkaline Alluvial Soil under mixed herbage.

pH Values.	No. of Soil Samples.	No. of Wormcast Samples.
7.2	—	1
7.3	—	3
7.4	4	4
7.5	2	—
Total Samples	6 (Av. pH 7.45).	8 (Av. pH 7.33).

The first and most important fact which these data establish is the considerable change in the reaction of acid soils effected by the earthworms, amounting to 0.75 pH in one instance. The change in reaction will be more readily appreciated if the differences in the negative logarithmic values given in Table III. are presented in the form of specific acidities (*cf.* Table V). These show that the effect is more marked the more acid the original soil, and that whereas the acidity of the soil is almost invariably decreased, the effect on alkaline soils may be to diminish the alkalinity (Table IV. B & fig. 2).

In the case of soil (1) the specific acidity was 79.4, so that in this case the earthworm action has resulted in a diminution of nearly 75 per cent.

FIG. 2.

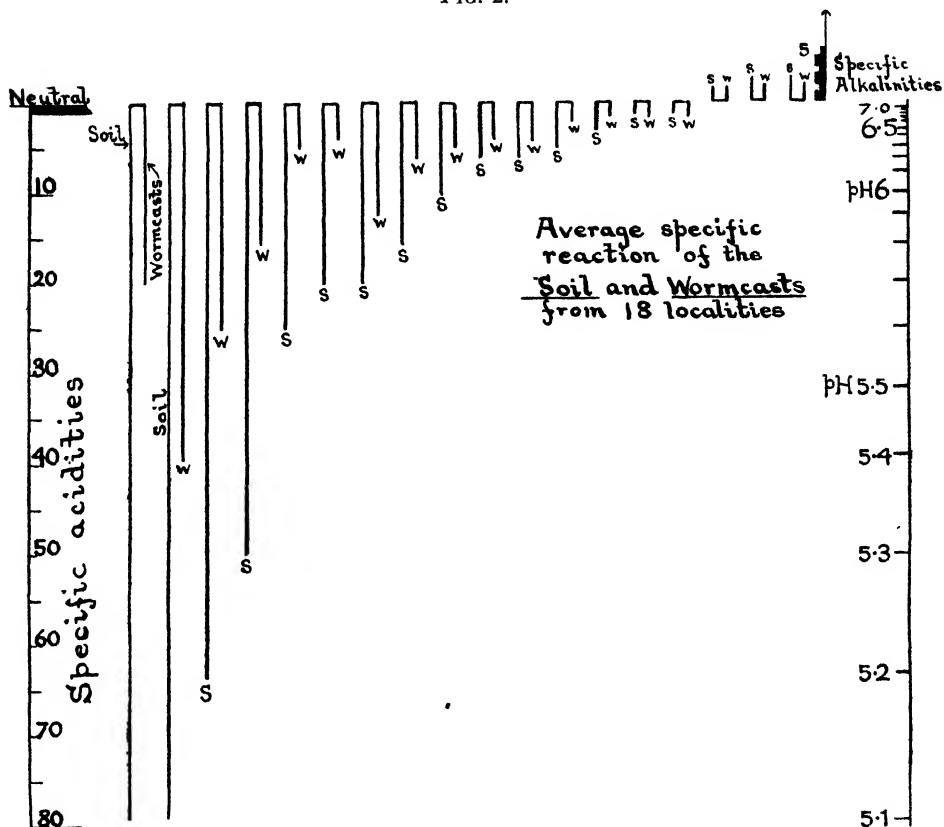


TABLE V.

Differences in Specific Acidity between Soil and Wormcasts.

(Neutral Water pH 7.03=1.)

1. <i>Festuca Agrostis</i> . Loc. A.	Difference in sp. Acidity . . .	-59.4 (S-W)
2. <i>Calluna-Triodia</i> .	" " "	-39.6
3. <i>Quercus Robur-Corylus</i> . Wood.	" " "	-38.0
4. <i>Festuca-Agrostis</i> . Loc. B.	" " "	-25.1
5. <i>Q. Robur-Corylus</i> . Wood.	" " "	-14.0
6. Nardetum.	" " "	-16.0
7. <i>Polytrichum juniperinum-Agrostis</i> . Loc. B.	" " "	-7.4
8. <i>Q. sessiliflora</i> .	" " "	-9.5
9. Pasture, Colney Heath.	" " "	-5.0
10. " Hertford Heath.	" " "	-2.3
11. " Holmwood.	" " "	-2.3
12. <i>Polytrichum-Agrostis</i> . Loc. A.	" " "	-3.0
13. <i>Q. Robur-Corylus</i> .	" " "	-1.58
14. Scrub, Markyate.	" " "	+1.2
15. <i>Q. Robur-Corylus</i> .	" " "	+0.32
16. Chalk pasture.	Difference in sp. Alkalinity . .	0.0
17. Alluvial meadow.	" " "	-0.4
18. Chalk pasture.	" " "	-0.4

Range .00-59.4.

Mean Difference = 12.9.

In the course of these estimations no attempt was made to distinguish between the various British species of Earthworm, and it is not improbable that these are capable of modifying the reaction in different degrees. Even, however, were the same species involved, the effect on different soils of the same original acidity might be expected to vary. For, though many soils are strongly buffered, the degree of the buffering is often very different in soils of the same original reaction.

As to the manner in which earthworms effect the change, Ray Lankester showed in 1864 (Q. J. M. S. vol. iv. p. 258) that the *oesophagus* of the earthworm bears three paired diverticula whose epithelium secretes calcareous particles (*cf.* also Beddard, Camb. Nat. Hist. p. 359), and Darwin long ago suggested that these might serve to neutralize the so-called Humic acids.

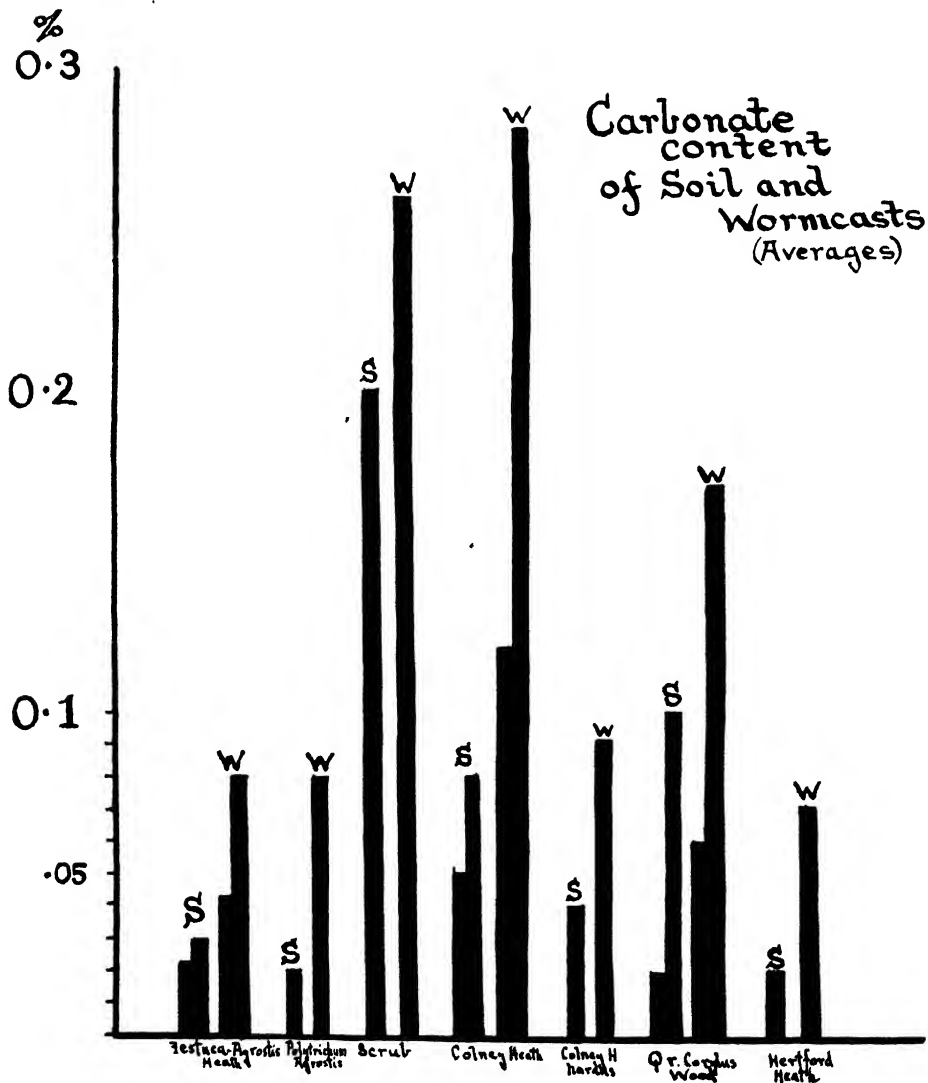
That this suggestion was justified, the above results would appear to show fully. However, the final proof was obtained by placing worms in a soil of known reaction and determining that of the wormcasts formed. The soil was carefully mixed, but at the time the wormcasts were collected the soil reaction showed a small range, namely from pH 6.6 to pH 6.8 with 6.66 as the mean value (specific acidity = 2.25). The wormcasts exhibited a range from pH 6.9 to pH 7.1 with a mean value of pH 7 (specific acidity = 1). The experimental conditions here precluded the possibility of the surface soil being mixed in the digestive tract of the worm with subsoil substance. The writer has elsewhere shown (*loc. cit.* Annals of Botany, vol. xxxvi.) that the later stages of decay are less acid than the earlier ones, and it is quite possible that during the process of digestion the chemical changes which the soil undergoes may lead to a decrease in acidity, but analyses of soil and wormcasts with respect to the carbonate content have shown that the latter normally contain an appreciably higher percentage than the soils from which they are respectively derived (*cf.* Table VI.). This is shown graphically in fig. 3.

TABLE VI.
Carbonate Content of Soils and Wormcasts.

	Per cent. Carbonates of Soil.	Per cent Carbonates of Wormcasts.
<i>Festuca-Agrostis</i>	0.022-0.03	0.047-0.07
<i>Polytrichum-Agrostis</i>	0.02 av.	0.08 av.
Markyate Scrub	0.20 av.	0.26 av.
Colney Heath, Loc. A	0.05-0.08	0.12-0.28
" " Loc. B	0.04 av.	0.09 av.
<i>Quercus Robur-Corylus</i> . Wood	0.02-0.10	0.06-0.17
Hertford Heath	0.02 av.	0.07 av.
Mean values	0.050 %	0.124 %

Apart, then, from the cultivating action of worms and the attrition of the soil particles due to their very muscular gizzard, the change which they effect on the reaction tends towards a reversal of the natural reaction gradient in uncultivated soils. Considerable evidence has accumulated in recent years showing the importance of both the direct and indirect effects of reaction in determining the distribution of plants, and a similar relation would appear to exist between reaction and some animals.

FIG. 3.



Several years ago the writer drew attention to the poor soil Fauna of acid woodlands as compared with those in which the soil was neutral or alkaline,

a feature especially marked with respect to the Molluscan fauna. Atkins * has recently published data emphasizing the importance of this factor in the distribution of snails.

It is then clearly essential to know how far earthworms are affected by the reaction of the soil. S. H. Hurwitz performed experiments with *Allobophora fatida* ("The Reaction of Earthworms to Acids," Proc. Amer. Acad. vol. xvi. pp. 67-81, 1910), in which the tips of suspended worms were dipped into dilute solutions $\frac{M}{100}$ of Hydrochloric, Nitric, Sulphuric, and Acetic acids. The time which elapsed, before contraction resulted in the withdrawal of the worm from the solution, was determined for a number of individuals, and it was found that the reaction time diminished with the increasing dissociation, thus indicating a considerable sensitiveness to the hydrogen-ion concentration. Similar experiments performed by A. T. Sohl ("Reactions of Earthworms to Hydroxylions," Journ. Amer. Physiology, vol. xxxiv. pp. 384-404, 1914) on the same species showed a correspondingly diminishing "reaction time" with increasing concentration of Hydroxyl ions. These experiments taken together appear to warrant the suggestion that an approximation to equality in the concentration of Hydrogen and Hydroxyl ions is the optimum condition for these animals. Arrhenius has performed experiments with both *Pericheta indica* and *Lumbricus terrestris*, in which soils were rendered artificially acid or alkaline. Both species were subjected to a range from pH 3 to pH 10, and at the end of a few days live individuals remained only in the soils which were very slightly acid or neutral (pH 6-pH 7).

The conditions in all these experiments, however, were clearly very artificial, so that observations were made by the writer on natural areas of varying reaction, the number of worms being determined both by actual counts of the earthworms in a cubic foot of soil, and by enumerating the freshly-formed wormcasts on a square yard. The average values and the observed range on each of the areas examined is shown in Table VII. It will be noted that broadly there is a diminution in numbers on either side of the neutral region (with respect to the diminution at pH 7.0 this is probably accidental; cf. below).

TABLE VII.
Earthworm Frequency in Natural Soils of varying pH.

Real acidity (pH)	5.7	6.2	6.4	7.0	7.2	7.4
Av. Earthworms per square yard {	1	3.2	35.2	9.3	144	19.0
Observed range.....	0-1	0-11	13-60	7-18	72-260	5-29
Av. per acre	0-484	15,488	170,386	45,012	696,960	91,960

* Atkins, W. R. G., & M. V. Lebour, in Scient. Proc. Roy. Dublin Soc. xvii. (1923) pp. 233-240.

This relation to reaction probably accounts for the rarity of earthworms in some siliceous areas. According to Darwin, for instance, earthworms are practically absent from the Welsh hills, where the soils most commonly exhibit an acid reaction. Similarly, earthworms are apparently infrequent in the very alkaline peat of true fens, though they may be present in considerable numbers in fen peat from which the alkaline salts have been partially leached, or in fen peat of naturally mild reaction.

But acidity or alkalinity are by no means the only factors which govern the distribution of earthworms, and amongst other conditions the proportion of organic material and the water content of the soil would seem most important. Darwin regarded Henson's figure (*Zeitsch. für Wiss. Zool.* Bd. xxviii. 1877) of nearly forty thousand worms per acre as very exceptional, but much higher frequencies have been observed. Thus in a locality with nearly neutral reaction, moderately high water content, and a high organic content the writer found a frequency of nearly 700,000 earthworms per acre. Some little-known observations of Dr. Brett may be quoted in this connection (*Trans. Herts. Nat. Hist. Soc.* 1883). This observer counted the worms in an area of one square yard of soil, dug out to a depth of three feet, in four different locations in a garden. The figures obtained range from sixty to one hundred and eighty earthworms per cubic yard. The latter number represents about 870,000 earthworms per acre, and it is pertinent to note that the location was a vine border where an approximately neutral reaction and a high organic content are essential to successful production.

As already indicated, an increase of organic content is frequently accompanied by an increased acidity and is usually correlated with a high water content. Despite, however, the suitability of the habitat in two of these respects, we find the reaction factor apparently dominating the frequency of the earthworms. Acidity (or alkalinity) would then appear to be a "master factor" in the distribution of these animals. It is significant in this connection that a very marked increase in the number of earthworms was observed to follow the application of lime to a garden soil well supplied with organic material but distinctly acid in reaction.

The writer has suggested that all natural soils tend to become more and more acid with increasing age, and this edaphic succession is accompanied by changes in the character of the vegetation (*cf. Journal of Ecology*, vol. ix. 1922). The fact that earthworms do not occur where the subsurface is appreciably acid shows that their effect on this edaphic succession is to cause a retardation in the establishment of the reaction gradient, but it does not appear probable that the increasing acidity of the surface can be permanently checked by their influence. This conclusion seems to be indicated by the much more acid character of wormcasts on acid soils than on those which are less acid or neutral. Further work may, however, show that a given species produces wormcasts of a much narrower range of reaction.

But, even if the effect be but a retardation and not a complete check to the edaphic succession, the importance of earthworm action in relation to vegetation may obviously be considerable.

To summarize, then, the main conclusions :—

- (a) Wormcasts, as compared with the soil from which they are derived, are usually less acid (or less alkaline), the reduction amounting in some cases to as much as 75 per cent.
- (b) Wormcasts commonly contain a higher proportion of carbonates than the surface soil.
- (c) The organic content of wormcasts is very high, indicating that the effects produced operate on that layer of the soil which is normally most acid.
- (d) The frequency of earthworms in natural soils appears to be greatest in those which are approximately neutral in reaction, and to diminish as the acidity or alkalinity increases. Other favourable factors are high water content and a high organic content.
- (e) Earthworms may thus have a marked effect on vegetation and retard the "edaphic succession."

The conclusions (a) to (c) are unaffected by the fact that the different species of earthworms were not distinguished. It is not improbable that the frequency in relation to the factors under (d) may vary with the species, and that their effects (e) may be of varying magnitude, though the data obtained would seem to indicate that such a difference, if it exists, is one of degree rather than of kind.

On the Cuticles of some Recent and Fossil Fagaceæ.

By HELENA BANDULSKA, A.R.C.S., M.Sc., F.L.S.

(PLATES 39, 40, and 6 Text-figures.)

[Read 6th March, 1924.]

Introductory.—In a previous investigation (Bandulska, 1923) of the cuticles of certain dicotyledonous fossil leaves from the Bournemouth Eocene, attention was concentrated on their structure, and their relationships were not discussed. The first part of the present paper deals with evidence for the inclusion of one of the described leaves, i. e. *Dicotylophyllum Stopesii* Band., in the genus *Nothofagus* Blume based on a study of the cuticular structure of recent *Nothofagus* leaves. The material used in the investigation of the recent cuticles was obtained from Kew and the British Museum, and was treated in the manner described in my former paper. The second half of the paper describes the cuticular structure of various recent species of *Fagus* and records a fossil *Fagus* with cuticle preserved, from the Eocene of Bournemouth.

I. THE GENUS *NOTHOFAGUS*.

Nothofagus is a subantarctic genus confined to southern South America, New Zealand, Tasmania, and eastern Australia. Of the species studied, *N. Dombeyi*, *N. betuloides*, *N. procera*, and *N. antarctica* are South American; *N. Solanderi*, *N. fusca*, *N. Menziesii*, and *N. Blairii* occur in New Zealand; *N. Moorei* is Australian, while *N. Cunninghami* is found in Australia and Tasmania.

The leaves vary in average length from 1.15 cm. in *N. Cunninghami* to 11.5 cm. in *N. Moorei*; their width ranges from .7 cm. (*N. Dombeyi*) to 4 cm. (*N. Moorei*). The margin is usually serrate, crenate, dentate or irregularly lobed, except in *N. Solanderi*, *N. Moorei*, and *N. Blairii*, where it is entire. The number of secondary veins on each side of the midrib may be as few as two or three (*N. betuloides*) or as many as seventeen (*N. procera*), and these make angles with the midrib ranging from 31° (*N. Solanderi*) to 52° (*N. procera*). For further details of habit, external characters, and distribution of *Nothofagus*, see Elwes & Henry 1908, Cockayne 1921, and Hooker 1840, 1844, and 1852.

Detailed Account of the Cuticles of the different Species of Nothofagus.

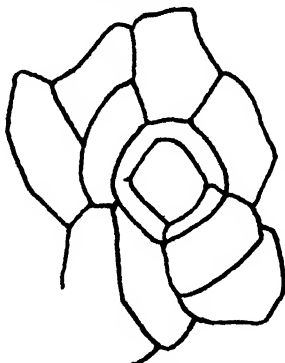
NOTHOFAGUS DOMBEYI Blume. *Lower Epidermis* (Pl. 39. figs. 1, 2).

The stomata are very definitely grouped into areas by small venules about 5 cells wide with somewhat elongated oblique-walled parenchymatous cells. On the venules, especially at the angles where they meet, are multicellular

hair-bases. Each stoma is bounded by a very thick cuticular rim, and is surrounded by a ring of parenchymatous cells irregular in size and grouping, and varying in number from 8–10. The average diameters of the guard cells are $\cdot 024$ mm. parallel to the long axis of the pore and $\cdot 025$ mm. at right angles to this.

Upper Epidermis.—The fine venules are 3–5 cells wide. Hair-bases occur, and consist of a varying number of radially-grouped cells (see text-fig. 1).

TEXT-FIG. 1.

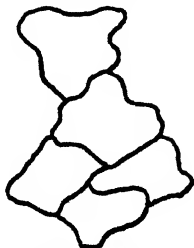
*Nothofagus Dombeyi.* $\times 768$.

Upper surface with hair-base and parenchyma.

NOTHOFAGUS PROCERA Oerst. *Lower Epidermis* (Pl. 39. figs. 3, 4).

The stomata do not show such definite groupings, nor are the epidermal cells arranged round each stoma as in *N. Dombeyi*. Each pore is bounded by a very thick cuticular rim. The guard cells have an average diameter of $\cdot 028$ mm. parallel to the pore, while at right angles to the long axis their average diameter is $\cdot 020$ mm. The epidermal cells have wavy walls.

TEXT-FIG. 2.

*Nothofagus procera.*

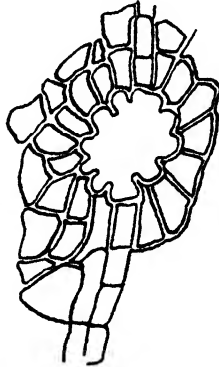
Parenchyma of upper surface.

Upper Epidermis.—The cells are far more regular in size and less sinuate in outline than those of the lower epidermis. A few hair-bases occur (see text-fig. 2).

NOTHOFAGUS BETULOIDES Blume. *Lower Epidermis* (Pl. 39. figs. 5, 6).

The stomata are grouped into areas by venules. They are very numerous and but few parenchyma cells occur between them. The guard cells are broad, with thickened cuticular poral rims and their line of junction is thickened, the thickening being continued like the top of a "T" piece at the

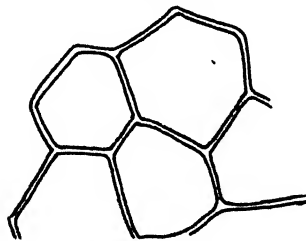
TEXT-FIG. 3.



Nothofagus betuloides. $\times 340$.
Resinous papilla base.

outer edge of the curve of the two guard cells. Each pair of guard cells is surrounded by 8–12 radially-grouped epidermal cells. The average diameter of the guard cells parallel to the pore is $\cdot 032$ mm., and at right angles to the pore is $\cdot 030$ mm. The venules are 4–12 cells wide, and consist of parenchyma which is somewhat elongated towards the middle of the venules. There are numerous papilla bases on the venules, frequently where veins meet. Each papilla base consists of a radiating group of about 20 somewhat elongated cells whose radial and cross walls bordering the opening are very thickened (see text-fig. 3).

TEXT-FIG. 4.



Nothofagus betuloides.
Parenchyma from upper surface.

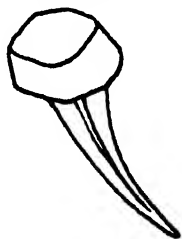
Upper Epidermis.—The veins bear papilla bases. The parenchyma cells are much larger than those of the lower epidermis (see text-fig. 4).

NOTHOFAGUS ANTARCTICA Forst., var. *ULIGINOSA*, A. DC. *Lower Epidermis* (Pl. 39. figs. 7, 8).

The stomata are grouped into areas by delicate venules 3-4 cells wide which bear numerous 2-celled hairs, each with a bulbous basal cell and an elongated very thick-walled terminal cell. Each stoma is surrounded by a group of 5-9 radially-disposed parenchymatous cells. The stomata vary much in size. They have a very thick cuticular poral rim, but no well-marked T-shaped thickening at the junction of the guard cells. The average diameters of the guard cells are .027 mm. by .025 mm. On some of the veins there are little mound-like groups of cells, radially arranged, which appear to be the bases of much larger multicellular hairs or emergences.

Upper Epidermis.—The parenchymatous cells are distinctly larger than those of the lower surface. The venules bear numerous 2-celled hairs whose average distance apart is .076 mm. (see text-fig. 5).

TEXT-FIG. 5.



Hair of *Nothofagus antarctica*.

The length of the hairs above the base is very variable. The venule cells are practically the same size as those of the lower epidermis, their average diameters being equal.

NOTHOFAGUS SOLANDERI Oerst. *Lower Epidermis* (Pl. 39. figs. 9, 10).

This is closely covered with tubular hairs arising from 5-8 radially-grouped cells. They much obscure the straight-walled parenchyma and enclose the stomata. These are very variable in size, and have very strongly-thickened poral rims but no "T" piece at the poles. Venules crowded with hairs intersect the surface. The guard cells measure on the average .019 mm. by .017 mm.

Upper Epidermis.—The cells are thick-walled with an occasional hair-base among them, but these are very few and bear no hairs. This xerophytic species is, as regards its cuticular measurements, an aberrant type.

NOTHOFAGUS FUSCA Oerst. *Lower Epidermis* (Pl. 39. fig. 11).

The stomata are scattered and in less definite groups than is commonly the case, but are separated irregularly by venules of variable width. Hairs do not occur on the lower surface. The parenchyma between the guard cells is regular, abundant, and straight-walled. Each stoma is bounded by a very

thick cuticular rim and a thickened peg or knob occurs at both inner junctions of the guard cells, but the characteristic T-shaped thickening is not seen at the poles of the long axes in well-macerated material. The outer walls of the guard cells are very delicate, only taking up stains faintly, and their line of junction tends to break down. There is no obvious grouping of parenchyma cells about the stomata. The stomata are almost isodiametric and variable in size. Their average diameters are .025 mm. by .023 mm.

Upper Epidermis.—This consists of regular, straight thick-walled parenchyma crossed by venules bearing a very few hair-bases. The average measurements of the various cells of this species of *Nothofagus* are in striking agreement with those of the corresponding cells of *Dictylophyllum Stopesæ*.

NOTHOFAGUS MOOREI Krasser. *Lower Epidermis* (Pl. 39. figs. 12, 13).

This closely resembles *N. Menziesii* (see below). Here, as in the latter species, stomata and thick-walled parenchyma are in definite groups enclosed by a practically rectangular venule network, but the walls of the epidermal cells are straight, and those surrounding the stomata stain more deeply than the rest. Radiate groups of thick-walled cells suggesting resin papillæ or their bases occur scattered over the lower surface between the stomata and on the venules, in some cases overarching the stomata in a dome-like way. The guard cells, large but variable in size and frequently broader than long, have thickened poral rims but no definite "T" piece at their junctions. Each stoma may be compared to a jewel set in a claw ring, for the radiate walls of the surrounding cells are ridged and grip the stomata like claws. The average diameters of the stomata are .029 mm. by .035 mm.

Upper Epidermis.—This is composed of thick and straight-walled parenchyma and ill-defined venules bearing scattered bulbous 2-celled hairs, each seated on a base of about 10 radiating cells. The bulbous basal cell stains very deeply.

NOTHOFAGUS MENZIESII Oerst.—Hooker says that this species is very similar to some of the states of *N. Cunninghami* of Tasmania (Hooker, 1844), but the cuticular structure is quite distinct.

Lower Epidermis (Pl. 39. figs. 14, 15).—This is a very beautiful form, composed of groups of stomata and sinuate thick-walled parenchyma enclosed by venules, the cells of which are also sinuate and differ from the rest of the epidermal parenchyma only in the slightly larger size and greater elongation of the constituent cells. The stomata have extremely thick and wide cuticular rims and the guard cells have thickened junctions, in these respects much resembling *Dictylophyllum Stopesæ*. They are large, but variable in size and flattened at the poles. Their average diameters are .025 mm. by .0245 mm. There is no well-defined "T" piece.

Upper Epidermis.—Whereas the lower epidermis is characterized by the extreme sinuation of its cell walls, those of the upper epidermis are practically straight and are also extremely thick. Hairs of the bulbous 2-celled type occur here and there on the venules, which are not clearly defined.

NOTHOFAGUS CUNNINGHAMI Oerst. *Lower Epidermis* (Pl. 39. figs. 16, 17).

The hairless cuticle is tough and composed of regular thick-walled sinuate parenchyma and very numerous stomata, not sharply grouped. The guard cells have strongly thickened cuticular rims and thickened junctions forming the characteristic "T" piece, but the vertical limb of the "T" is frequently double. Four to six cells surround the stomata, but show no special differentiation or grouping. The guard cells measure on the average .026 mm. by .022 mm. No meshwork of venules crosses the epidermis.

Upper Epidermis.—Regular small cells very slightly or not at all sinuate form the cuticle of the upper surface. There are a few tubular thick-walled pointed hairs arising from deeply-staining spherical bases among these cells. The whole hair is two-celled, the terminal cell having a very narrow cavity and resembling a typical sclerenchymatous cell. Precisely the same kind of hair, but in far greater abundance, is seen on the upper surface of the cuticle of the leaf of *N. obliqua*. *Nothofagus Cunninghami* can be distinguished from *N. Menziesii* by its scattered stomata, which in *N. Menziesii* are definitely grouped. The stomata of the latter species are isodiametric; those of the former are longer than they are broad. *N. Cunninghami* bears more hairs on its upper surface than *N. Menziesii*.

NOTHOFAGUS BLAIRII Cockayne. *Lower Epidermis* (Pl. 39. figs. 18, 19).

Very hairy with numerous delicate stomata and regular straight, thin-walled parenchyma. The guard cells have strongly-thickened poral rims but neither thickened junctions nor "T" piece, and are surrounded by undifferentiated parenchyma. The average diameters of the guard cells are .025 mm. by .023 mm. The hairs are of the typical two-celled form—a deeply-staining bulbous basal cell surmounted by a long-pointed thick-walled terminal cell.

Upper Epidermis.—The thick-walled parenchyma is crossed by a few thick-walled, narrow, ill-differentiated venules 4–5 cells wide. No obvious hairs are present, but a few collar-like hair-bases occur.

Summary of the General Characters of Nothofagus Cuticles.

Species of *Nothofagus* are characterized by the presence of practically isodiametric stomata in definite groups. The individual stomata are variable in size with strongly-cuticularized poral rims, accompanied frequently by cuticular thickenings at the junctions of the guard cells, and by a horizontal strip of cutin at the poles of their long axes so that a "dagger"-like appearance is presented. The completeness of the cutinization seems to vary inversely with the hairiness. The average diameters of these cells are in

close agreement in most species. The epidermal cells may be sinuate or straight. In some species the upper epidermis has straight walls, the lower, sinuate walls (*N. Menziesii*), or both surfaces may exhibit sinuations (*N. procera*), or both upper and lower cuticle may consist of straight-walled cells (*N. Dombeyi*). The upper epidermis of all the recent species of *Nothofagus* lacks stomata.

DICOTYLOPHYLLUM STOPESÆ Bandulska.—In external form the fossil leaf previously described (Bandulska, 1923, p. 244) resembles several species of *Nothofagus*, but this in itself is inconclusive. The cuticular structure, however, indicates the close affinity of these leaves. The average diameters of the isodiametric guard cells of *D. Stopesæ* are in close agreement with those of *Nothofagus*, and the size of the individual stomata of *D. Stopesæ* shows the same extreme variability. The fossil form exhibits, too, the thickened poral rim and the cutinized "dagger" at the junctions of the guard cells. The lower epidermal cells are very slightly sinuate. The upper epidermis consists of parenchyma with hair-bases, but one preparation showed two or three stomata at one end.

Fragments of the cuticle of this species differing only in the somewhat greater sinuation of its epidermal cells have been isolated recently from the Bournemouth Beds (Pl. 39, fig. 20).

The only recorded fossil species from Europe, so far as I am aware, which may show affinity with *Nothofagus* is *Fagus pygmaea*, described by Unger (1867) from beds probably of Lower Miocene age at Kumi in Greece. This he considers resembles most closely *Nothofagus obliqua*. He describes it as a small ovate-elliptical serrate leaf, and certainly its external form is like *Nothofagus*, but it has recently been referred by Fritel (1921) to *Quercus oreadum* Sap. The presence of a species of *Nothofagus* in beds of Eocene age in England is therefore of extreme interest.

II. THE GENUS *FAGUS*.

Fagus is a genus with a wide distribution, occurring throughout western Europe, central and western China, Japan, Asia Minor, and North America. Of the species investigated, *Fagus sylvatica* is spread over western Europe, *F. Engleriana* is found in central China, *F. Sieboldii* in Japan. *F. grandifolia* is the beech tree of N. America, and *F. orientalis* that of Transcaucasia, while *F. sinensis* is the common beech of central and western China, and is, by some authorities, thought to be synonymous with *F. Engleriana*.

The leaves vary in length from 3 cm. to 15 cm., *F. sylvatica* being the largest-leaved species and *F. Sieboldii* the smallest. The width varies from 2.5 cm. to 10 cm. In shape the leaves are ovate (*F. sylvatica*), obovate (*F. orientalis*) or oblong (*F. Engleriana*), with a base which is rounded or more or less tapering (*F. orientalis* and *F. grandifolia*) and an apex which is acute or acuminate (*F. grandifolia*, *F. Sieboldii*). The margin may be faintly

sinuate (*F. sylvatica*) or dentate, coarsely serrate (*F. grandifolia*), or weakly toothed and indented (*F. Engleriana*). The midrib is prominent, with secondaries varying in number in the different species from 5–10 as in *F. sylvatica* or from 7–15 as in *F. grandifolia*. The range of angle made by the secondaries with the midrib is 36° to 46° .

The leaves are delicate in texture, with the exception of *F. grandifolia* which is tough. In these species of delicate texture the upper surface is less delicate than the under surface. For further details of external structure, see Elwes and Henry 1908, Engler 1897, 1900–1901.

Detailed Account of the Cuticles of the different Species of Fagus.

FAGUS SYLVATICA Linn. *Lower Epidermis* (Pl. 39. fig. 21; Pl. 40. fig. 22a).

The stomata have thick cuticular rims, which persist uninjured when over-maceration of the leaf destroys the parenchyma. The guard cells are broad and flattened at their junction, which is very delicate and not thickened, thus differing markedly from species of *Nothofagus*. They are surrounded by 4 or 5 epidermal cells. The average diameters of the guard cells are $\cdot 028$ mm. by $\cdot 022$ mm. The epidermal parenchyma consists of very irregular cells, and may or may not be sinuate. The veins are 4–5 cells wide. Hairs of two kinds occur:—(1) Short, tubular, deeply staining, arising from a thick-rimmed basal cell upon which two or three cells are superimposed and vermiformly curved. These are scattered among the epidermal cells. (2) Slenderer, very long, colourless hairs, which arise from a distinct base which bears terminally a single long thick-walled cell. These hairs appear to be restricted to the larger veins, and their base consists of the junction of three or four vein cells.

Upper Epidermis (Pl. 40. fig. 22b).—There are a very few hair-bases similar to those of the long hairs of the lower epidermis among the parenchyma cells, while the same hair-bases are abundant on the larger venules. Very numerous hair-bases are found at the junction of upper and lower epidermis.

FAGUS ENGLERIANA Seemen (6797 Brit. Mus. Herb.).

Lower Epidermis.—Delicate, readily over-macerated (Pl. 40. figs. 23a, 23b). The stomata occur in roughly quadrangular groups surrounded by venules bearing numerous hairs and hair-bases, and hairs are also numerous among the stomata. The guard cells and hairs stain deeply pink with saffranin, while the parenchyma does not take up the stain. Four to six parenchyma cells surround each stoma, but there is no definite grouping or special differentiation. The pores are minute; the guard cells very small and slightly depressed at their junctions, with very delicate outer walls. Two convex thickened strips of cutin meet at the pore and diverge slightly towards the

poles. Some stomata show three bars of thickening which radiate from the pore to each long axis, where the guard cells are flattened. The guard cells have an average diameter of .016 mm. parallel to the pore, while at right angles to the long axis their average diameter is .015 mm. The parenchyma is practically straight-walled. The hair-bases are tubular and composed of two or three cells, forming a linear series, seated on a thickened basal collar cell. The tip is usually torn. The venules are three to five cells wide and the venule cells are somewhat elongated and unthickened.

Upper Epidermis (Pl. 40. fig. 24).—This is composed of straight-walled regular parenchyma. Hair-bases are very numerous both on the parenchyma and in the numerous intersecting venules.

FAGUS GRANDIFOLIA Ehrenb. The cuticle is resistant to maceration, not delicate.

Lower Epidermis (Pl. 40. figs. 25, 26 a).—The stomata are in groups interspersed with slightly sinuate parenchyma and surrounded by venules. The guard cells are broad, frequently broader than long. The small pore has a slightly thickened poral rim, and the outer walls of the guard cells are stronger than is the case in most species of *Fagus*. The junctions of the guard cells are strongly thickened, the cutin passing outwards just round the horns of the crescents and forming a thin horizontal bar, so that the T-shaped cutinization characteristic of some species of *Nothofagus* is produced, but is less obvious than in *Nothofagus*. The average diameter of the guard cells parallel to the pore is .017 mm., and the average diameter of the guard cells across the pore is .019 mm. The parenchyma cells are very variable in size, sinuate, and tough-walled. The venules are 2–3 cells wide, and consist of more elongated, less sinuate, and narrower cells than those of the parenchyma. A few tubular hairs and hair-bases occur on the venules.

Upper Epidermis (Pl. 40. fig. 26 b).—This consists of moderately thick-walled sinuate parenchyma crossed by venules bearing tubular hairs and hair-bases.

FAGUS ORIENTALIS Lipsky (5113 Brit. Mus. Herb.).

Fagus orientalis is apparently synonymous with *F. sylvatica* var. *longepedunculata* Hausk. Lipsky says the leaves of *F. orientalis* do not differ from those of *F. sylvatica* except that those of the former are sometimes a little more leathery.

The cuticle is very delicate, easily over-macerated (see Pl. 40. figs. 27, 28).

Lower Epidermis.—Stomata variable in size, with finely sinuate parenchyma interspersed between them. There are four or five cells, more or less definitely arranged round each stoma. The stomata have slightly thickened cuticular rims, and the guard cells have very slightly thickened junctions and a thinner cutinized border round the outer rim. They are practically isodiametric, sometimes broader than long and flattened at the poles of the long axes.

Their average length is .025 mm. and their average width across the pore is .023 mm.; thus the stomatal measurements of *Fagus orientalis* are in complete agreement with those of *Fagus sylvatica*. Tubular hair-bases resting upon five to seven radially-grouped cells occur on venules and parenchyma.

FAGUS SIEBOLDII Endl. (5796 Brit. Mus. Herb.).—The cuticle is delicate easily over-macerated.

Lower Epidermis (Pl. 40 figs. 29, 30).—This bears very numerous long tubular hairs and hair-bases on the larger venules, the hairs resting on five to seven radially-disposed and thickened epidermal cells. There are no hairs among the epidermal cells, nor is there the network of venules forming areoles so characteristic of other *Fagus* species. The stomata are extremely delicate, and are surrounded by parenchyma whose walls are thin and practically straight. The stomata have slightly thickened cuticular rims, but their outer walls are very delicate and their junctions are not thickened; hence there is no suggestion of the cutinized “dagger” or “T” piece so common in *Nothofagus*. The epidermal cells are somewhat radially disposed round the guard cells. The average length of the guard cells is .021 mm. and their average width is .021 mm.

Upper Epidermis.—This consists of nearly straight-walled parenchyma. Narrow venules, two cells wide, bearing occasional hair-bases, cross the surface at wide intervals. Their cells are thick-walled, elongated, and somewhat irregular in size and shape.

FAGUS SINENSIS Oliver (4409 Brit. Mus. Herb.).

Lower Epidermis (Pl. 40. figs. 31, 32).—Very delicate stomata are enclosed by long, tubular, thick-walled unicellular hairs. The guard cells vary in size, and are sometimes wider than long. Their outer walls are very delicate, but their junctions are slightly thickened, forming a short “T” piece, and the poral rims are also slightly cuticularized. The average diameters of the stomata are .026 mm. by .027 mm.

The parenchyma is regular, moderately thick-walled and straight, though occasionally a wall shows one sinus. This is strikingly different from the parenchyma of the upper surface, which is markedly sinuate. The venules are 2–5 cells wide, elongated, and very thick-walled, some cells showing spiral thickenings. They are not seen in well-macerated material. Hairs occur among the stomata and scattered through the parenchyma as well as on the venules. The hairs arise from a base of about seven radially-grouped cells, and when the hair is torn away these surround a circular space.

Upper Epidermis (Pl. 40. fig. 33).—The parenchyma is regular and very sinuate, and crossed by widely-separated venules, two cells in width.

Summary of the General Characters of the Cuticles of the Genus Fagus.

The cuticles have broad, usually isodiametric stomata flattened at the poles, the individual stomata varying in size and being restricted to the lower surface, where they are usually in definite groups. The poral rims of the guard cells are slightly thickened; their line of junction is usually delicate, or with very slight thickening, but with no definite "dagger" or "T" piece of cutin except in *F. grandifolia*. The absence of this "dagger" of cutin and the extreme thinness of the outer walls of the guard cells broadly distinguish the genus *Fagus* from *Nothofagus*, but species of the latter approximate to the former in this respect, while a few species of *Fagus* exhibit all the cutinizations of *Nothofagus*, although the thickenings are much slighter. As far as cuticular structure is concerned, the species of *Fagus* and *Nothofagus* form a continuous series. The guard cells of *Fagus* tend to be somewhat smaller than those of *Nothofagus*, and there is less average agreement in stomatal measurements between the different species than is the case in *Nothofagus*.

The epidermal cells of *Fagus* may be sinuate or straight, or one surface only, either upper or lower, may be sinuate. Thus *F. sinensis* has a sinuate-walled upper epidermis and a straight-walled lower epidermis. *Fagus Engleriana* has both surfaces composed of straight-walled or minutely sinuate cells. *Fagus sylvatica* is very variable in the amount of sinuation of its cells; therefore sinuation in these genera is not a character of systematic importance.

Taking certain pairs of closely similar forms about whose relationship there has been considerable argument, we may note that the stomata and epidermal cells of *Fagus sinensis* are larger than those of *Fagus Engleriana*, there are far fewer hairs in the former, and the upper epidermis is sinuate.

When we compare *Fagus sylvatica* with *Fagus orientalis*, we find that though both these species have delicate cuticles, there is more cutinization in *F. orientalis* than in *F. sylvatica*, for not only has the former stomata with thickened rims, but there are also slight thickenings at the junctions of the guard cells, which have, moreover, some horizontal cutinization. In *Fagus sylvatica* the line of junction of the guard cells is very delicate, and there is little or no horizontal cutinization. The epidermal cells of the upper surface are larger in *F. orientalis* than in *F. sylvatica*, and they are finely sinuate on both surfaces.

The epidermal cells and venule cells of the recent and fossil forms have all been measured and tabulated, but no general conclusions can be drawn except that on the whole the cells are the same size throughout the two genera.

FAGUS BOURNENSIS, sp. nov. (Pl. 40. figs. 34-36.)

Occurrence. Bournemouth Beds, Eocene.

Locality. Cliffs between Alum Chine and Middle Chine.

External Characters (Pl. 40. fig. 34).—Leaf simple; apex and part of right half missing. Length 6 cm., width 4.5 cm. Margin sinuate dentate. Base

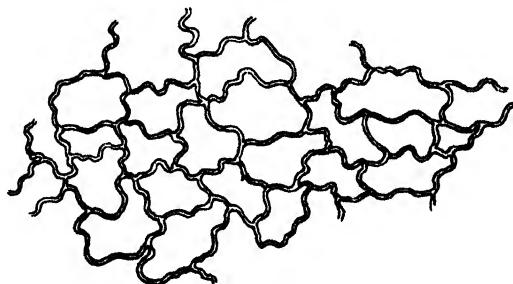
slightly tapering. Midrib strongly marked with eight lateral veins on each side. Range of angle made by lateral veins with midrib 37° – 52° . Average angle 43° .

Cuticular Structure (Pl. 40, figs. 35, 36).—The cuticle is delicate and readily over-macerated as in the living species of *Fagus*.

Lower Epidermis.—Stomata are confined to the lower surface. They vary in size. The guard cells are broad and flattened at the poles of their long axes. They have inner thickened cuticular rims and are horizontally cutinized at each end. Their line of junction is not strongly thickened, and is easily destroyed by over-maceration. Four epidermal cells usually surround them. The cells constituting the epidermal parenchyma have sinuate walls; the venules are about two cells wide, their walls being also sinuate, but the venule cells are narrower than those of the epidermis. Hair-bases are scattered over venules and parenchyma, and consist of a thick-rimmed basal collar, somewhat raised upon a number (about 8) of radially-disposed cells. The average diameters of the guard cells are .027 mm. by .017 mm.

Upper Epidermis (see text-fig. 6).—This consists of sinuate parenchyma crossed by venules. There are hair-bases on the venules and among the parenchyma cells.

TEXT-FIG. 6.



Upper surface of Fossil *Fagus* from Bournemouth.

SUMMARY.

An investigation of the leaf of *Dicotylophyllum Stopesæ* shows that it must be referred to the family Fagaceæ, and included in the genus *Nothofagus* as distinct from *Fagus*. Hence it is suggested that it be called *Nothofagus Stopesæ* (Bandulskæ).

Both the external form and the cuticular structure of the fossil named *Fagus bournensis* indicate its close connection with *Fagus* rather than with *Nothofagus*. The general external characters of the Bournemouth species are in striking agreement with those of *Fagus sylvatica*. The cuticle is more hairy, has somewhat smaller stomata, narrower venules and smaller epidermal cells, and is more xerophytic in habit. It is in all probability a specifically distinct form, and I therefore propose to call it *Fagus bournensis*.

Kräusel (1919) describes *Fagus* leaf-impressions from the Tertiary of Silesia, and considers that *F. sylvatica* and *F. ferruginea* both occur there, with transition forms between the two. The cuticular measurements of *F. bournensis* certainly suggest an intermediate position for this fossil between *F. sylvatica* and *F. ferruginea* (= *F. grandifolia*).

Acknowledgements.—I have to thank Dr. Smith Woodward of the Geological Department of the British Museum and Dr. Rendle of the Botanical Department for allowing me the use of these departments. I owe thanks also to Mr. W. N. Edwards for many helpful suggestions and criticism, and to Mr. F. W. Edwards for photographing my preparations.

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EXPLANATION OF THE PLATES.

PLATES 39, 40.

Nothofagus Dombeyi.

- Fig. 1. Under epidermis, $\times 135$. Groups of stomata. Multicellular hair-base on venule.
- Fig. 2. Under epidermis, $\times 540$. Four stomata varying in size, with very thick poral rims and a thickened dagger at the junctions of the guard cells.

Nothofagus procera.

- Fig. 3. Under epidermis, $\times 135$. Scattered stomata, and sinuate parenchyma crossed by venules.
- Fig. 4. Under epidermis, $\times 540$. Three stomata are shown, varying in size and with strongly thickened poral rims.

Nothofagus betuloides.

Fig. 5. Under epidermis, $\times 135$. Groups of stomata divided by venules. One resinous papilla seated on venule.

Fig. 6. Under epidermis, $\times 540$. Two large stomata showing broad guard cells and T-shaped thickenings at the junctions.

Nothofagus antarctica.

Fig. 7. Under epidermis, $\times 135$. Stomata in groups and venules bearing bulbous two-celled hairs.

Fig. 8. Under epidermis, $\times 540$. Stomata with thickened poral rims.

Nothofagus Solanderi.

Fig. 9. Under epidermis, $\times 135$. Numerous hairs surrounding small stomata.

Fig. 10. Under epidermis, $\times 540$. Stomata with thickened poral rims and deeply-staining tubular hairs.

Nothofagus fusca.

Fig. 11. Under epidermis, $\times 540$. Stomata with thickened poral rims. Non-sinuate parenchyma.

Nothofagus Moorei.

Fig. 12. Under epidermis, $\times 135$. Stomata in definite groups and thick-walled parenchyma. Note that the epidermal cells are straight-walled.

Fig. 13. Under epidermis, $\times 540$. Stomata with thickened poral rims and varying in size. No "T" piece of cutin.

Nothofagus Menziesii.

Fig. 14. Under epidermis, $\times 135$. Two groups of stomata. Note waved character of epidermal and venule cells.

Fig. 15. Under epidermis, $\times 540$. Stomata varying in size and flattened at the poles, with thick cuticular rims and thickened junctions.

Nothofagus Cunninghami.

Fig. 16. Under epidermis, $\times 135$. Stomata not sharply grouped, with thickened rims and thickened junctions forming the characteristic "T" piece. Thick-walled sinuate parenchyma.

Fig. 17. Under epidermis, $\times 540$. Three stomata showing the double vertical limb of the "T" piece of cutin and very thick poral rims.

Nothofagus Blairii.

Fig. 18. Under epidermis, $\times 135$. Very delicate stomata and thin-walled parenchyma with numerous hairs.

Fig. 19. Under epidermis, $\times 540$. Stomata with thickened poral rims but neither thickened junctions nor "T" piece. Stomata very variable in size.

Dicotylophyllum Stopesæ.

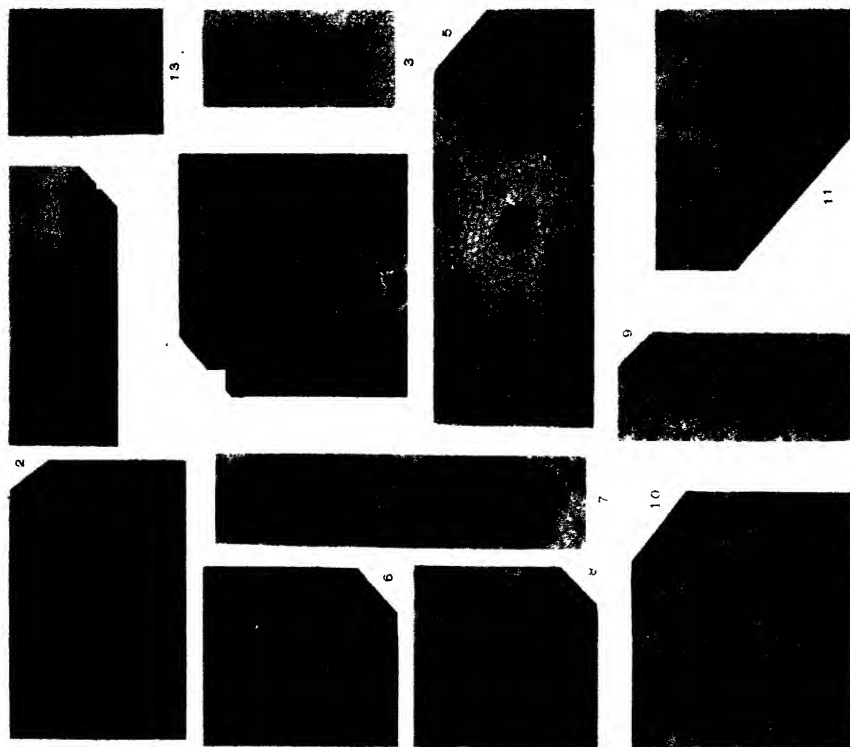
Fig. 20. Under epidermis, $\times 540$. Stomata with thick poral rims and thickened "T" piece at the junction of the guard cells. Compare the stomata with those of *Nothofagus Dombeyi*.

Fagus sylvatica.

Fig. 21. Under epidermis, $\times 135$. Delicate, broad, flattened stomata. This preparation shows straight-walled parenchyma.

Fig. 22 a. Under epidermis, $\times 540$. Two stomata with thickened poral rims and delicate junctions. Sinuate parenchyma.

Fig. 22 b. Upper epidermis, $\times 135$. Sinuate parenchyma and vein with hair-bases.



CUTICLES OF FAGACEAE

F W Edwards, Photo.

RECENT AND FOSSIL

Zined Collette Co. Engraving



34



35



23 a



22 b



27



36



26 a



25



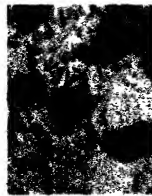
22 a



29



30



23 b



28



24



33



32



26 b



31

Fagus Engleriana.

- Fig. 23 *a*. Under epidermis, $\times 135$. Delicate stomata surrounded by tubular hairs.
 Fig. 23 *b*. Under epidermis, $\times 540$. Four small stomata, depressed at the junctions of the guard cells.
 Fig. 24. Upper epidermis, $\times 135$. Compare this with *Fagus sinensis*.

Fagus grandifolia.

- Fig. 25. Under epidermis, $\times 135$.
 Fig. 26 *a*. Under epidermis, $\times 540$. Broad guard cells with thickened junctions and small pores. Slightly sinuate parenchyma.
 Fig. 26 *b*. Upper epidermis, $\times 135$.

Fagus orientalis.

- Fig. 27. Under epidermis, $\times 135$. Stomata with slightly thickened cuticular rims and flattened at the poles. Finely sinuate parenchyma.
 Fig. 28. Under epidermis, $\times 540$. Three stomata. Delicate, very slightly sinuate parenchyma.

Fagus Sieboldii.

- Fig. 29. Under epidermis, $\times 135$. Very delicate, showing hairs and thin-walled parenchyma and stomata.
 Fig. 30. Under epidermis, $\times 540$. Very delicate stomata, variable in size, surrounded by thin straight-walled parenchyma.

Fagus sinensis.

- Fig. 31. Under epidermis, $\times 135$. Stomata enclosed by long tubular hairs.
 Fig. 32. Under epidermis, $\times 540$. Delicate stomata and thin-walled straight parenchyma.
 Fig. 33. Upper epidermis, $\times 135$. Compare this with *Fagus Engleriana* (fig. 24).

Fagus bournensis.

- Fig. 34. Complete leaf, V. 15900, British Museum (Nat. Hist.) Geol. Dept.
 Fig. 35. Cuticle of under epidermis, $\times 135$. Venule with hair-bases. Stomata of varying size. Sinuate parenchyma.
 Fig. 36. Cuticle of under epidermis, $\times 540$. Broad guard cells of varying size, with inner thickened cuticular rims, slightly thickened junctions, and horizontal cutinizations. Sinuate parenchyma.

The Germination of *Hippuris vulgaris* L. By R. D'O. GOOD, B.A.
(Communicated by Dr. A. B. RENDLE, F.R.S., P.L.S.)

(With 3 Text-figures.)

[Read 13th December, 1923.]

ALTHOUGH much work has been done upon the embryology of *Hippuris vulgaris* L., there does not seem to be any detailed account of the germination or of the many interesting features exhibited during the process. Irmisch (in Bot. Zeit. xvii. p. 353) refers to it briefly, while Glück (in Wasser- und Sumpfgewächse, vol. iii. p. 257) touches upon one or two points. Further details are given by Fauth (in Bot. Cent. xiv. p. 349), but here again the account is very incomplete.

Hippuris vulgaris (Mare's Tail) is a plant of somewhat uncertain systematic position. Bentham and Hooker place it in the family Haloragidaceæ, while Engler and Prantl include it in a family of its own, the Hippuridaceæ. It is a water plant with a creeping rhizome and erect shoots bearing whorls of subulate leaves. The upper portions of the shoots emerge above the surface of the water. The flowers, which are protogynous and anemophilous, are borne in the axils of the leaves on the aerial shoots. Each flower consists of a single epigynous stamen and one carpel, having one pendulous anatropous ovule. The fruit is a drupe. The Mare's Tail is almost cosmopolitan in distribution, and occurs fairly commonly over nearly the whole of the British Isles. Its morphology and affinities are dealt with in detail by Schindler in Engl. Bot. Jahrb. xxxiv. Beibl. 77. Incidentally this writer states that fertilization is rare and that ripe fruits are produced only in suitable years.

The fruits from which the germination was studied were all taken from the gizzards of two species of wild duck shot on Loch Spynie, Banffshire, Scotland. Four samples were used, three from teal and one from a tufted duck. In each case the hard endocarps, together with a little grit, formed the whole contents of the gizzards. In all cases the outer fleshy coverings of the drupes had been worn away by grinding action within the birds. Except in one case, the birds had been shot some considerable time before, and the fruits had since been allowed to dry naturally.

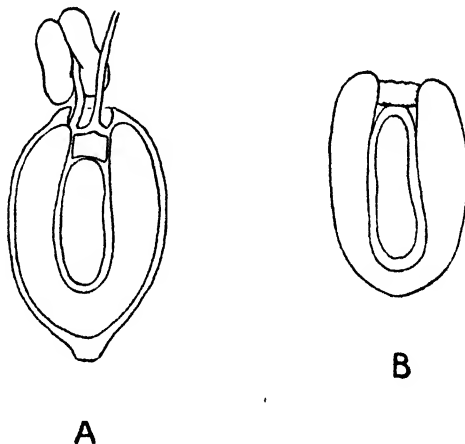
These four samples were sown under similar conditions upon a layer of mud at the bottom of beakers containing ordinary tap water and left at ordinary room temperature. In their dry condition the fruits floated on the surface, but within a day or so became waterlogged and sank to the bottom.

The germination results obtained are here given in tabulated form :—

Sample.	Bird.	Bird shot.	Fruits sown.	1st germination.	Remarks.
1.	Teal	8 Aug. '23.	13 Aug. '23.	22 Aug. '23.	Nearly all germinated by 1 Sept. '23.
2.	Teal	23 Feb. '23.	31 Aug. '23.	12 Sept. '23.	Almost completely failed to germinate.
3.	Tufted Duck	1921.	31 Aug. '23	5 Sept. '23.	Nearly all germinated by 9 Sept. '23.
4.	Teal . , . . .	21 Feb. '23.	11 Sept. '23.	21 Sept. '23.	Only 7 fruits germinated from this sample.

The number of fruits in the samples averaged about 60.

FIG. 1.



A. Longitudinal section of ripe fruit of *Hippuris*.

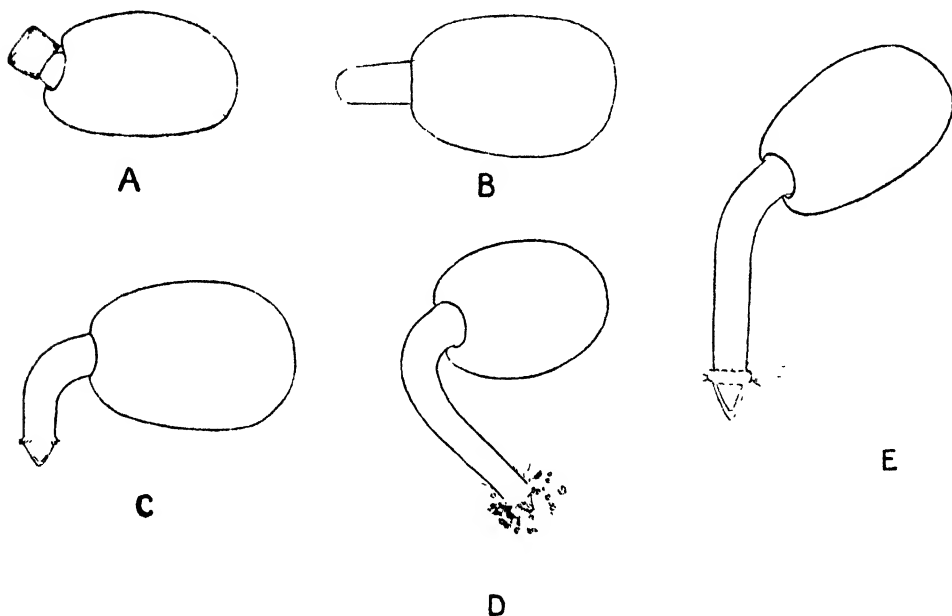
B. Longitudinal section of fruit removed from gizzard of a Teal.

The ripe drupes of *Hippuris* are ovoid in shape, and consist of a thick hard endocarp covered by a thin fleshy exocarp. The endocarp is incomplete at the upper end, and the foramen is closed by a plug or stopper of hardened tissue. The whole bears a remarkable resemblance to a corked ovoid bottle. The growth of the ovule and the formation of the stopper is fully described by Juel (in *Nova Acta Reg. Soc. Sci. Upsaliensis*, ser. 4, vol. ii. no. 11). Earlier papers on the same subject are those of Unger (in *Bot. Zeit. Jahr.* vii.) and Tulasne (in *Ann. Sci. Nat.* sér. 3, tom. xii.). Juel shows that the stopper is formed from the hardened under part of the horizontal funicle and the hardened upper part of the integument in the vicinity of the micropyle. Above the stopper comes the soft tissue of the ovary wall, or receptacle, from which the style arises,

When the ripe fruit falls from the parent plant it floats on the water for a short time, and allows a certain measure of water-dispersal. Bird-dispersal also occurs, as in the cases here described, but whether either method is more normal is uncertain.

The large embryo in the seed is straight, and lies with its hypocotyl directly below and directed towards the stopper. The first step in germination is the gradual pushing out of this stopper by the elongation of the hypocotyl. This action is a leverage rather than a direct push, and in most cases the stopper remains attached at one point of its circumference to the endocarp. The hypocotyl now appears as a blunt white body protruding

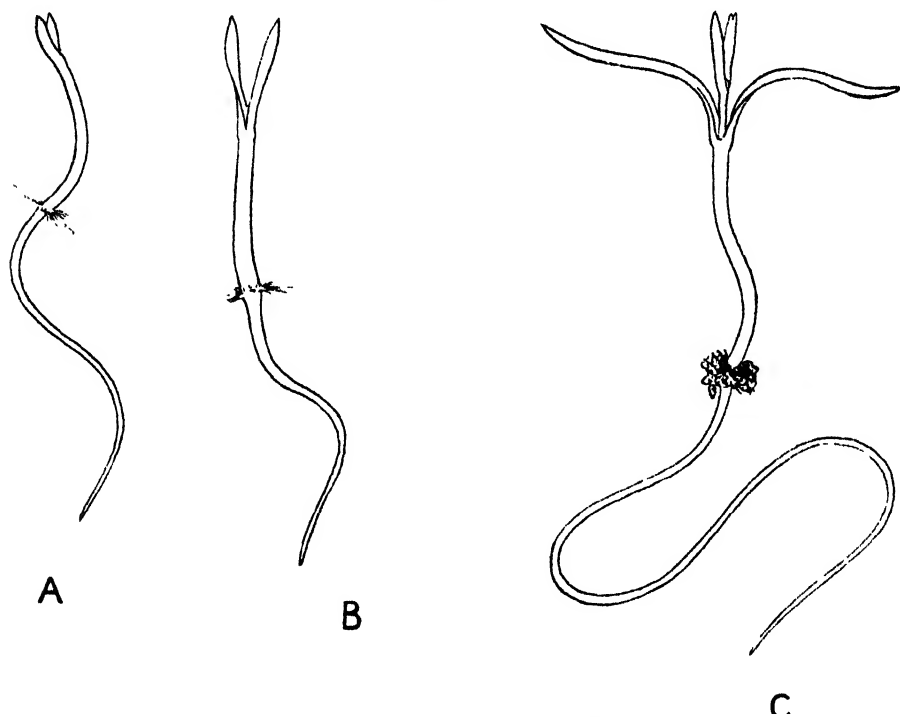
FIG. 2.

A-E. Early stages in germination of *Hippuris*.

from the foramen of the fruit. Within a day or two it undergoes a positively geotropic curvature so that the tip is directed vertically downwards. Soon after this a ridge appears just behind the tip, and rapidly develops into a collar bearing a ring of horizontally-spreading root-hairs. Such a ring of hairs arising from the collet is not uncommon, especially among aquatic plants. Warming (in Bot. Zeit. Jahr. xli. p. 202) gives a list of plants in which it occurs. At this stage the upper part of the hypocotyl becomes green. Beyond the hairs the tip of the hypocotyl becomes differentiated into a central core and an outer transparent sheath. This is the initiation of the radicle, which now quickly elongates and penetrates the mud.

When the radicle is established the upper part of the hypocotyl, which has meanwhile been slowly elongating, undergoes another and reverse curvature and becomes vertical, bearing the endocarp on its tip. The cotyledons are still inserted in the fruit and absorb the thin layer of endosperm, which contains reserve food in the form of aleurone and fatty oils (Fauth, *loc. cit.*). After the straightening of the hypocotyl, the cotyledons begin to elongate towards their bases and to emerge from the fruit until only the tips are imprisoned. At length the fruit is completely levered off, apparently by the divergence or spreading of the cotyledons, and falls clear

FIG. 3.

A-C. Later stages in germination of *Hippuris*.

of the seedling. The two cotyledons now spread out at right angles to the axis of the young plant. From this point the vegetative axis of the mature plant develops in the axil of the cotyledons, and the first leaves appear. These resemble the ordinary axial leaves and are borne in whorls, but are much smaller. They bear scattered stomata and a few of the peltate hairs so characteristic of the plant (see Solereder, 'Systematic Anatomy of the Dicotyledons,' Engl. ed. vol. i. p. 337).

Glück (quoted on p. 443) states that the first whorl may have 2, 3, or 4 leaves, and that the second whorl has only 2 leaves, while the immediately subsequent

ones have 3 or 4. From an examination of some 50 seedlings it would appear that these numbers are rather arbitrary. Taking into consideration only the first, second, and third whorls, by far the most common formation is one of 4 leaves. The number may be, and often is, anything from 2 to 5, but 4 predominates. With this formation a definite leaf mosaic is obtained, the leaves of *alternate* whorls lying immediately above one another. It also appears that the whorls, at any rate in young seedlings, are the result of successive decussate leaf pairs with alternately very long and very short internodes. In older plants, and in the upper shoots, this arrangement is modified, and the whorls consist of from 6 to 10 leaves.

The growth of the young plant has now been described up to the appearance of the fourth whorl of leaves. Shortly after this stage the first pair of lateral shoots appear in the axils of the cotyledons. At a slightly earlier stage many of the seedlings produce, also from the cotyledonary axils, a root which bends down and grows straight towards the mud. Branching of the primary root sometimes occurs, but appears to be a somewhat abnormal proceeding. The successive and opposite curvatures of the hypocotyl in the early stages deserves particular notice.

There is considerable divergence of opinion as to the meaning and function of the ring of hairs produced at the collet. Warming (*loc. cit.*) discusses the subject shortly, and states that Klebs considers that their functions are absorption and anchorage. The former is very probable, but since the hairs are produced on the surface of the mud, the exact method of anchorage is difficult to understand. Samsoë Lund (in Bot. Tid. Copenhagen, Bd. v.) goes further, and, in the case of *Batrachium heterophyllum*, suggests that, by accumulating particles of mud, the hairs increase the weight of the seedling and prevent it from rising to the surface when the heavy empty fruit is dropped off. In the case of *Hippuris* the hairs do undoubtedly collect particles, and when the endocarps drop off the seedlings have a tendency to rise, but this is prevented not by the ring of hairs but by the penetration of the radicle, which is by then well developed, into the mud. Further, the horizontal spread of the hairs is such as to prevent penetration into the mud, and it seems that it is this prevention which is their chief mechanical function. Owing to the heaviness of the fruit lying on the mud, any growth of the hypocotyl is in the nature of a thrust away from the fruit. In the absence of the hairs, therefore, growth of the hypocotyl will lead simply to its penetration into the mud until only the fruit remains above. Under such circumstances the fruit can only be set free from the seedling by the withdrawal of the cotyledons under the mud, where their later functions would be impossible. It seems, therefore, that the function of the hair-ring is to form a platform or base away from which the upward growth of the shoot can take place, and by means of which the cotyledons can become erect and develop in their natural position. In the case of such

a loose substratum as mud, which is easily silted, any mechanism which tends to keep the chlorophyll-bearing organs above the surface must be of some importance. In ordinary land plants the radicle is, of course, firmly held in position by the soil particles.

Mrs. Arber, in her book on "Water Plants," and others have stated that the fruits of *Hippuris* winter on the mud and germinate in the following spring. To test this statement ripe fruits of the current season were obtained through the kindness of Mr. Gilbert Carter of the Cambridge Botanic Garden, and immediately sown under conditions similar to those mentioned above. At the time of writing (end of November) no germinations had occurred*. This helps to confirm the above views, since it can hardly be expected that germination would commence in mid-winter. Fauth (*loc. cit.*) states that he has seen germination in progress in April, and also mentions that fruits dried over the winter and sown in March germinated in June. It will be remembered that the seedlings here described were from fruits which had been naturally dried for some time.

Fischer (in *Ber. Deut. Bot. Ges.* xxv. p. 108) states that the fruits of many aquatics, including *Hippuris*, can be kept for years, without germinating, in pure (distilled) water. If, however, fermentation occurs, the action of the H^+ and OH^- ions stimulates the dormant protoplasm to growth. On the other hand, Crocker (in *Bot. Gaz.* xlv. p. 376) considers that abundance of oxygen and water are chiefly necessary.

Hippuris fruits are covered when ripe by a complete outer covering of thin-walled tissue, and it appears that germination does not occur until this layer, which seals the enclosed embryo, is removed. Its removal may be under water by the ordinary processes of decay or by mechanical means within the gizzards of birds. In either case germination seems to follow readily. Probably the removal of the outer tissues allows the external factors of stimulation, whatever they may be, to act upon the embryo. In the presence of the outer layers of the fruit the actual movements of germination, such as the pushing out of the stopper, must be greatly impeded, if not actually prevented. If this explanation of the delay in germination is acceptable, it is correlated with the fact that the fruits of *Hippuris* ripen late in the season, so that immediate germination would leave the young seedlings to pass the winter in a very critical stage of development.

In conclusion, there seems no reason for believing that passage through the alimentary canal of a bird is in itself a necessary preliminary to germination.

My thanks are due to Mr. E. H. Ellis of the Natural History Museum for his assistance in connection with the work here described.

* These fruits eventually germinated in July, 1924.

Studies in the Micropalæontology of Postglacial Deposits in Northern Scotland and the Scotch Isles, with especial reference to the history of the woodlands. By G. ERIDTMAN. (Communicated by Dr. E. J. SALISBURY, F.L.S.)

(With 20 Figures in the text, and Map—PLATE 41.)

INTRODUCTION.

THIS paper is based upon material collected during a journey in Scotland and the Scottish Isles in July 1922. The object of this journey was to obtain evidence as to the development of postglacial woodlands from the peat mosses of Scotland, and compare it with the evidence from the peat mosses of the south-west of Sweden, previously obtained and published by the author in 1920 and 1921. Further, by the investigation of an isolated group of islands (*e.g.* the Shetlands or the Faroes*), it might be possible to determine to what extent pollen carried long distances by the wind (150–200 km.) would influence a fossil pollen-flora.

My route was as follows (map, Pl. 41):—

July 3rd–8th.—*Achnasheen*, Ross-shire, situated near the watershed between the Moray Firth and the Minch.

„ 6th.—*Strathcarron*, Ross-shire (on the west coast).

„ 9th–10th.—*Isle of Skye*.

„ 11th–18th.—*Isle of Lewis*.

„ 19th–20th.—*Helmsdale*, Sutherlandshire.

„ 21st–29th.—*The Orkneys*, mainland; 28th, Westray.

„ 30th–Aug. 1st.—*The Shetlands*, mainland.

The method employed in my investigations was that worked out by Lennart von Post, State Geologist of the Geological Survey of Sweden. The first account of this method was given in a paper by von Post, which was read at the meeting of Scandinavian naturalists at Christiania in 1916 [“Skogsträdspollen i sydsvenska torfmosselagerföljder” (The pollen of forest trees in the mosses of South Sweden), *Forh. ved 16. Skand. naturforskeimöte 1916*]. Later, Dr. von Post published a series of papers dealing with the method and showing how it could be applied in many ways: *e.g.*, “Postarktiska klimattyper i södra Sverige” (Postarctic types of climate in Southern Sweden), *Geol. Fören. Förhandl. Bd. 42, 1920*, and “Ur de sydsvenska skogarnas historia under postarktisk tid” (summary: Some features of the

* Unfortunately I was unable to visit the Faroe Islands.

regional history of the forests of southern Sweden in postarctic time), *ibid.* Bd. 48, 1924. Investigations have also been carried out by the disciples of von Post. As one of these, I would here express my best thanks to Dr. von Post, to whom I am greatly indebted, not least for the interest he has shown in the plan of my researches in Scotland.

As the two leading authorities on the study of micro-fossils (and especially of fossil pollen-grains), upon which von Post's method of pollen-analysis is based, we must mention Prof. Dr. C. A. Weber of Bremen and Prof. Dr. G. Lagerheim of Stockholm. The former as early as 1893, in his paper "Ueber die diluviale Vegetation von Klinge in Brandenburg und über ihre Herkunft" (Engler's Bot. Jahrbücher, xvii. Beibl. 40), counted pollen-grains and calculated the proportion between *Pinus* and *Picea* pollen. He laid stress upon the suggestion that pollen-grains must, on the average, give a truer picture of general vegetation of a neighbourhood than the remains of wood and fruits, for the occurrence of these in the water depends on chance (*l.c.* p. 8). Prof. Lagerheim has carried out a great number of important and most accurate enumerations of pollen-grains, and has studied the occurrence of other micro-fossils, especially parts of cryptogams. Also he has made micro-analyses from Scottish peat deposits, the results of which are published in the work of Samuelsson: "Scottish Peat Mosses" (Bull. of the Geol. Inst. Uppsala, vol. x. 1910). Because of his remarkable knowledge of micropalæontology, Dr. Lagerheim has for many years been able to help and encourage many peat geologists. He has also done much towards perfecting methods of analysis. For several years I have had the opportunity of working at the Botanical Institute of the University of Stockholm under the direction of Prof. Lagerheim; also a short time ago (Easter 1923) I visited Prof. Weber in connection with some peat investigations in North-West Germany. To both of them I express my respectful thanks.

To Mrs. E. M. Reid, Milford-on-Sea, I remain especially indebted for having most kindly undertaken the correction of my English.

To Dr. J. Horne of Edinburgh I am greatly indebted for invaluable help in the way of good advice and the kind loan of geological maps. For help in various forms I have also to thank Dr. A. Gravelin, Head of the Geological Survey of Sweden, Dr. J. Gunn of Edinburgh, Mr. D. Mackenzie of Stornoway, Prof. P. Quensel of Stockholm, Dr. E. J. Salisbury of Radlett, and Prof. Sernander of Uppsala.

G. ERDTMAN.

The Botanical Laboratory,
The University, Stockholm
Dec. 29th, 1923.

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1. METHOD OF SURVEY*.

A. The Field Work.

a. Equipment.

The following outfit was carried for the field work :—A peat bore of the Hiller pattern, a smaller model (*vide* Haglund, 1909) with 7 links to 1 m., which allowed samples to be taken from peat mosses to a depth of 7 m. This bore, kept in a leather case and carried by a strap over the shoulder, is very easy to handle, and I was able to do all the work unaided. I also used a boring-stick, length 1 m.; a turf-knife for cleaning the walls of the peat-hags and for cutting sections; oakum for cleaning the container of the bore; a three-foot rule; a diopter compass; a sitometer (*vide* Rübel, 1922, p. 140); an aneroid; forceps and spatula for taking the turf out of the container of the bore; small glass tubes, 7.5 cm. long and 1.3 cm. inside diameter, corked at both ends, in which to keep the samples; lastly, small bags of strong, brown paper in which to carry the samples to the laboratory for washing or

* The greater part of the subject of this chapter has already been published, though in a short form, by von Post (1916 *a* and *b*). These papers are, however, written in Swedish, and thus not accessible to the greater part of non-Scandinavian readers.

chemical examination. For taking levels and measuring sections I used a Tesdorpf tube. The very short time at my disposal did not allow of such measurements, or of analyses of the recent peat-moss vegetation. For these a simple folding wooden square of 1 sq. m. is used (*cf.* Du Rietz, 1921, fig. 20).

b. *The Field Work proper.*

After making trial borings, a bore is made in the most representative spot, at first to a depth of 50 cm. The container of the bore has a length of 30 cm., and we thus get a peat core of this length. As a rule two samples are to be taken from every core, which, in this case, would come from a depth of about 25 and 45 cm. below the surface of the peat moss. Next, borings are made to 100, 150, 200 cm., etc., below the surface. In some cases, especially when dealing with sediments or with peat which has taken a very long time to form, it is better to take 3 to 5 or more samples from every core, also to make borings every 25 cm. When these manipulations are carried out with due cleanliness, there is no risk of getting dirty specimens. However, if there are peat-hags or cuttings in the neighbourhood, these are to be preferred. Such sections seem to be more common in Scotland than in Sweden, partly owing to the greater shallowness of the Scottish peat. (For a more detailed description, see Erdtman, 1921, pp. 15-16.)

B. *The Laboratory Work.*

When making preparations for microscopical examination, a very small amount of the samples taken from each end of the peat pillar and enclosed in the little glass tubes is laid on a slide and boiled with 10 per cent. caustic potash (KOH) *. When the greater part of the water has evaporated, a drop of glycerine is added. A part of the cooked substance is then laid on another slide and covered with a cover-glass. The pollen-grains are then counted by the use of the micrometer stage of the microscope, and for each specimen analysed I write a record; for example, the following:—

13. x. 1923.		167 (Skye).	
<i>Alnus</i>	19 = 11 per cent.	Tetrads of <i>Ericaceæ</i> .	
<i>Betula</i>	130 = 74 per cent.	<i>Sphagnum</i> spores.	
<i>Pinus</i>	14 = 8 per cent.	Grass pollen.	
<i>Quercus</i>	5 = 3 per cent.	Filicinean spores without exosporium.	
<i>Ulmus</i>	7 = 4 per cent.	Fragments of needles of <i>spongæ</i> .	
Total	175 = 100 per cent.	<i>Nuphar</i> pollen.	
<i>Corylus</i>	1 = sporadic.	<i>Polypodium vulgare</i> (spore).	
PF (pollen frequency) =	560 (0.6).	<i>Glaettrichia</i> sp.	

* Minerogene earths are often better treated with HFl (compare Assarsson and Granlund, 1924).

The PF (frequency of pollen per preparation; 560 in the above record) indicates the number of pollen-grains in a unit of area (N.B. The pollen of forest trees; not *Corylus*, *Salix*, *Rhamnus*, etc.). The unit I have chosen is 1 sq. cm. PF is by no means an exact number, because the thickness of the preparations may vary considerably. After practice, however, the preparations can be made, as a rule, of almost uniform thickness, in which case the PF numbers may have a certain importance.

To get almost exact percentages it is sufficient to count about 150 pollen-grains; but even if only 50 pollen-grains are counted, the result is of value (*vide* Jessen, 1920, p. 23, note). Auer (1923, pp. 347-349), in his explorations of peat in northern Finland, expressed the PF by using a scale with 5 degrees (1=very rare, 5=very common).

In the records of analysis, after the PF numbers, I write, in brackets, the number by which the total of pollen-grains counted is to be multiplied so as to get the number 100; or, expressed in another way, the figure by which the number of pollen-grains of each species is to be multiplied so as to get the percentages of each species: for example, in one record we find PF=33 (2). There are here 33 pollen-grains per sq. cm., and the analysis is not quite reliable because only 50 pollen-grains were counted. In a second, PF=126 (1); here 100 pollen-grains were counted. In a third, PF is 88 (0.65); and thus about 155 pollen-grains were counted. As to the numbers in brackets, experience tells that 0-1 designates good, almost exact, analyses; 1-2 fairly good; 2-5 less good; and numbers >5 analyses in which the percentage figures are of little or no value.

The relative frequency-number of *Corylus* and *Salix*, also of other microfossils whose frequency one desires to express (e.g. *Nuphar* pollen, tetrads of Ericaceæ, spores, etc.), is calculated separately as a percentage of the total number of pollen-grains of the forest trees. Owing to the fact that *Salix* pollen somewhat resembles the pollen of certain plants with a very different systematic position, I decided not to count the pollen of *Salix* with the pollen of the forest trees as von Post and others had done previously and I myself did in 1921.

In Scotland I have found fossil pollen from all trees, *Picea* excepted, of which the pollen is met with in the peat mosses of Southern Sweden: *Acer*, *Alnus*, *Betula*, *Carpinus*, *Fagus*, *Fraxinus*, *Pinus*, *Quercus*, *Tilia*, and *Ulmus*; also in a few localities I have discovered *Ilex* pollen.

By means of the percentage numbers a *pollen-diagram* is constructed. "The relative frequency-numbers, which are produced for the pollen-species found in a sample investigated, constitute the *pollen-spectrum* of the sample. On the basis of a series of 'pollen-spectra' from a sectional boring in a bog, a pollen-diagram may be constructed, in which curves for the single species, or for a group of species, give both a visual representation of the composition of the pollen-flora and the oscillations as regards frequency which have taken place reciprocally between the pollen-curves during the formation

of the bog" (Jessen, 1920, p. 245). A more detailed account of the construction of pollen-diagrams is found on pp. 22-23 (Erdtman, 1921). One hundred micro-fossils, amongst others the above-mentioned pollen-grains, are figured in 'Arkiv för Botanik,' Bd. 18 (Erdtman, 1923 a). Docturowsky and Kudrajaschow (1923) have published 23 figures of forest-tree pollen.

2. PEAT MOSSES INVESTIGATED.

In modern peat-geology with its emphasis upon phyto-physiognomy, analyses of the recent vegetation are indispensable for a correct classification of the different kinds of sedentary (non-transported) and sedimentary material. As already mentioned, I had not enough time to make such analyses, and thus—even after the microscopic investigations I have made—I am unable to give all the deposits met with their descriptive names. "*Sphagnum-Scirpus cespitosus* peat," "*Calluna* peat," and so forth, are to be regarded therefore as provisional names.

It is a defect in Lewis's work ("The Plant Remains in the Scottish Peat Mosses") that he does not use a fixed terminology. In Part I. he distinguishes different kinds of peat, such as *Sphagnum* peat and *Scirpus* and *Sphagnum* peat; later on he also describes layers with *Pinus* and layers with *Empetrum* etc. In Part II., alone, he uses the terms "dominant" and "secondary" plants, in Part III. "characteristic" and "accompanying" plants. Finally, in Part IV. he returns very nearly to the terminology of Part I. This manner of description gives us, for instance, very little information about the sediments. That there must have been organic sediments at some of the places investigated is, however, shown by the presence of diatoms and certain macro-fossils, e. g. *Potamogeton*. The occurrence of sediments is also mentioned by Bennie, Reid, and others.

At this point I take the opportunity of defining, in accordance with von Post (1922), some of the organic sediments met with in Scotland.

1. **Clay-Gyttja** (Swedish "lerygttja").—The name "gyttja" (plur. gyttjas; Swed. "gyttjor") is applied to such sediments as give a green or greenish extract when treated with alkali. "**Dy**" treated in the same way gives an extract where brown is the prevailing colour.

Clay Gyttja is a dense, somewhat elastic substance, without evident phyto-structure, i. e. structure caused by plant-remains. It has a small content of sand or clay. The colour is yellow-grey or blue-grey with a suspicion of green. It turns white when dried. The alkaline extract is either greenish or colourless.

2. **Plankton-Gyttja**.—A dense, usually elastic, sometimes almost rubber-like substance, without phyto-structure. The colour is green (almost vivid), yellow-green, or brown-green of various shades. On exposure to the air it usually darkens rapidly, but, when dried, the bright colour returns. Alkaline extract green.

3. **Detritus-Gyttja**.—A dense, more or less elastic substance, without phyto-structure in the matrix, but often traversed by rootlets of *Phragmites* and *Equisetum*. The colour is brown, usually tinged with green of different shades. In the air it darkens rapidly, but, upon drying, the colour usually revives a little. Alkaline extract green or slightly brownish.

4. **Lake Dy** (Swed. "sjödy").—A dense substance, usually but slightly elastic, without phyto-structure in the matrix. The colour is brown or brownish black, with usually a slight tinge of green. It blackens rapidly in the air, and does not brighten, or scarcely brightens, upon drying. Alkaline extract a decided brown colour.

5. **Lime-Gyttja**.—A dense, usually elastic substance without phyto-structure in the matrix, but as a rule rich in shells of freshwater snails and mussels. The colour is whitish-yellow, reddish-yellow, yellow-brown, or of various greenish tints, often mottled. When heated with acid, it bubbles and hisses slightly.

In places Lewis speaks of "recent peat" without any accurate definition of the term. It would be better not to speak of "recent peat" at all, because it must always be doubtful where the boundary between recent and not recent is to be drawn. "*Recent*" is a term which it is only permissible to apply to the vegetation still growing on the surface of a peat moss. We may define as "*sub-recent*" material belonging to the "*förna*" [Hesselman, 1911; Sernander, 1918 = humus nekron; cf. also Moss, 1904, fig. 6; Lewis, 1904, p. 321; Paul, 1916 ("Latschenhumus"); Ramann, 1918, p. 70; C. Weber, 1903, p. 430 ("Streudecke")] if we are dealing with sedentary deposits, or material belonging to the "*äfja*" (Sern. *l. c.* = sapropel nekron) if we are dealing with sedimentary deposits. The term "*sub-fossil*" is not needed, as there is no reason why peat, pre-, inter-, and post-glacial, should not be called fossil. Some authors, indeed, apply the term *sub-fossil* to all remains found in postglacial deposits (cf. Paul, 1924); others only to those found in the Atlantic layers.

In a recent paper, Rigg (1922) describes a bog forest in the neighbourhood of Victoria, British Columbia, with lodgepole pine (*Pinus contorta*) dominant, Labrador tea (*Sedum granlandicum*), Shallon (*Gaultheria Shallon*), etc. These species are constituents of the *recent* vegetation. The floor of the pine forest is thickly covered with pine-needles mixed with a small amount of other material of vegetable origin. Under the surface decay has begun. The depth of the layer of pine-needles in various stages of decay is from 6 to 12 inches. This is the "*förna-layer*," or the *sub-recent* material, which often plays an important part in the forming of peat. Beneath this is a layer of old *Sphagnum* peat, usually 12 inches or more thick (= the *fossil* material). Logically this terminology should be applied without any restriction to all deposits, whatever their nature. T. Högbom, in his paper "Ancient inland

dunes of Northern and Middle Europe" (Geografiska Annaler, 1923), prefers to use the term "ancient" instead of "fossil"; but there is no reason why a pre-, inter-, or post-glacial seed, or bone or pollen-grain, should be called fossil, and a pre-, inter-, or post-glacial dune should not, unless it now continues in an active stage. There is, of course, a great difference between the dunes which Högbom describes and the dunes of older formations, the evidence of which may be obtained in some sandstones; but this difference must, however, be expressed in another way—for instance, with terms referring to the different physical conditions.

A. *Peat Mosses in Ross-shire (Achnasheen and Strathcarron).*

The general features of the stratification are given by Lewis (1906, 1911) and Samuelsson (1909). As to the vegetation of the peat mosses, compare also the papers of Hardy (1906) and Crampton and Macgregor (1913). One section south of Inchnadamff showed, according to Samuelsson (*l. c.* p. 210), the following strata (the determination of the pollen-grains was carried out by Prof. Lagerheim):—

- A. 80 cm. *Scirpus caespitosus* peat. Pollen of alder and elm.
- B. 50 cm. Forest peat, very rich in birch branches and twigs, and in the uppermost zone containing large pine-stools. Pollen of alder, birch, elm, hazel, pine.
- C. 40 cm. *Scirpus caespitosus* peat, very decayed. Pollen of birch, hazel, pine.
- D. 15 cm. *Carex* peat, containing *Eriophorum vaginatum* remains and very abundant *Empetrum* stems.
- E. 20 cm. *Carex* peat, containing a few birch twigs but no *Empetrum* stems.

According to Lewis (Part IV. 1911, p. 809) the usual depth of the peat in the neighbourhood of Poolewe is 6 feet, except in one or two spots which, as shown by the character of the deposits, occupy the sites of silted-up lochs. The uppermost layer is formed by *Scirpus caespitosus* and *Sphagnum*; then follows a layer with large stools and trunks of *Pinus* and fragments of *Betula* wood. He found, as did Lagerheim, that the peat lying immediately under the pine-stools contained numerous pollen-grains of pine (p. 811).

In East Sutherlandshire (Rhilochan) Lewis (IV. p. 812) found an Upper Forest with *Pinus* and a Lower Forest with *Alnus*, *Betula*, and *Corylus* (nuts abundant); in Goire Bog (East Ross) the Upper Forest also consists of *Pinus* remains, but no trace of the Lower Forest was found, the "second arctic bed" resting immediately on sand.

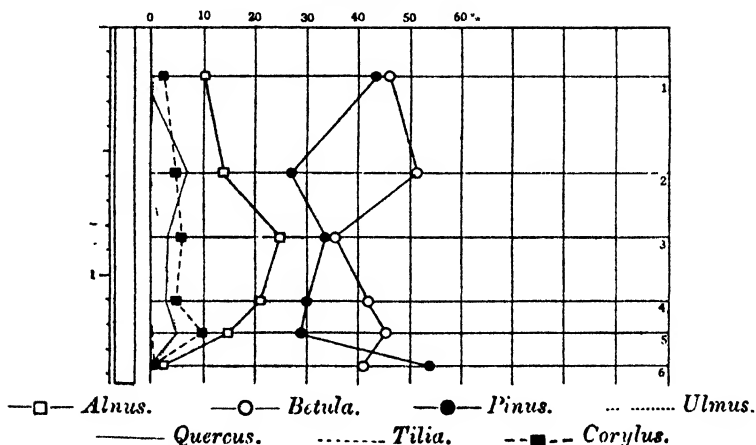
After this brief summary of the salient features of Lewis's work, I will describe the peat mosses investigated by myself (maps used: Ordnance Survey of Scotland, sheets 82 and 103).

PEAT MOSS No. 1. (Text-fig. 1.)

Situated near the sign ² (second terrace of freshwater alluvia) south of "S" in "Station" (Achnasheen Station), south of the R. Bran, which connects Loch a' Chroisg with L. Achanalt, this lake draining into Cromarty Firth. Altitude above sea-level about 150 m. Thickness of peat averaging 145 cm.

The surface of the moor was clothed with a *Calluna-Scirpus cespitosus* association with *Carex pauciflora*, *Drosera longifolia*, *D. rotundifolia*, *Erica Tetralix*, *Eriophorum vaginatum*, *Juncus squarrosus*, and *Narthecium ossifragum*. This peat moss is a typical "tourbière morte," and by process of erosion deep hags have been cut which sometimes reach the underlying sand. A great number of pine-stools rest upon this sand, and protrude about 60 cm. into the peat. The micro-analysis of the well-humified peat shows that the

TEXT-FIG. 1.



greater part has been formed by *Sphagnum*. In samples 1 and 2, *S. imbricatum* was noted. In the upper part of the peat, remains of *Scirpus cespitosus* and other species belonging to the recent vegetation were common. There is no trace of sand, not even in the stratum immediately above the sand.

If this bog were investigated by the old methods, the investigator would, almost certainly, have tried to explain the sequence of layers in the following way :—

- A. 85 cm. **Recent Peat**, consisting chiefly of *Sphagnum* with *Scirpus cespitosus* remains.
- B. 60 cm. **Upper Forest**, large stools of *Pinus*.
- C. (at 145 cm.) **Sand**.

If, however, we compare the pollen diagram (text-fig. 1) of this peat moss with the other diagrams, it becomes perfectly clear that the lowest layer (the layer from which sample 6 was taken) best corresponds with Lewis's Lower Forest Bed, despite the fact that Lewis never found pine in this bed. The

pollen character of the level from which sample 6 is taken is clearly defined. (In what follows, this zone will be referred to as the "A"-zone.) It shows a high frequency of *Pinus* (usually also of *Corylus*) and a low frequency of *Alnus*. In the stratum immediately below the A-zone, *Alnus* pollen disappears almost suddenly, *Ulmus* and *Betula* pollen often show a greater frequency, whilst the frequency of *Pinus* and *Corylus* becomes less. In, or above, but never below, the A-zone, *Tilia* pollen has been observed. As *Alnus*, *Betula*, and *Corylus* characterize the Lower Forest Bed, the pine layer described above must belong to this stratum; also because the pollen of *Alnus*, and a little further down that of *Corylus*, quickly disappears from the layers immediately below the A-zone.

The *Sphagnum* peat above the stool-layer must belong both to Lower and Upper Peat bog. No trace of a Second Arctic Bed is found. The pollen-flora of sample 1, with its relatively high frequency of pine pollen, seems to indicate that the layers near the present surface were formed at, or about, the time of the Upper Forest. The striking resemblance should be noted between this diagram and the lower part of diagram (text-fig. 5, p. 463) from a peat moss near Strathcarron, apparently still growing. This comparison strengthens the view that the moor No. 1, here dealt with, is a "tourbière morte" where new peat is not formed.

Pollen of *Tilia* is noted from sample 6; spores of *Polypodium vulgare* (by far the commonest pteridophyte micro-fossil in the Scottish peat mosses) from sample 2; spores of *Tilletia Sphagni* from sample 5; whilst *Assulina*, *Amphitrema*, and *Oribates* sp. were found in various samples.

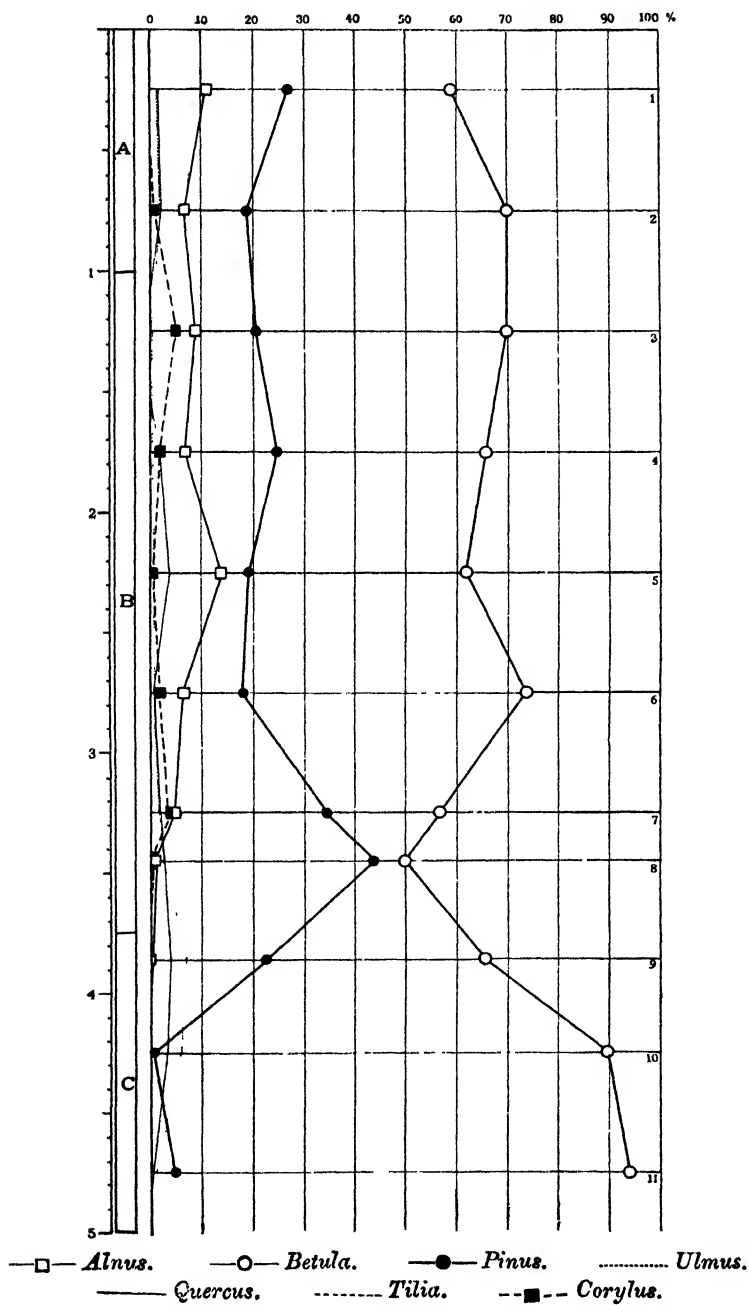
Thomas Brown (Geol. Mag. 1866) has described a buried forest near Loch Maree, not far away from Achnasheen. It exhibits almost the same features as described above. "The stools of the trees are wholly embedded in peat, varying from 18 to 36 inches in thickness. Beneath the peat is a bed of gravel, in the surface of which the trees appear to have grown. They were generally, if not exclusively, Fir, the natural tree of the Highlands."

PEAT MOSS No. 2. (Text-fig. 2.)

Situation: south-east of Achnasheen, about 2500 m. S.S.W. of Carn na Feith rabhain on a line connecting Desmuckeran with the most western point of Loch Bennacharain. Altitude above sea-level about 44 m.

The surface of this little peat moss—a silted-up loch—resembles at the present time a damp meadow. The form is almost circular, the diameter being about 150 m., and it is drained towards the North. A large amount of water flows from the S.E. towards the meadow, where it collects in a round hole close to the place where the boring was made, and from there passes away by subterranean drainage. It is surrounded by a wide tract of mountainous country, covered to a great extent with hill-peat, which bears striking evidence of great erosion. Among others, the following species were seen in the meadow:—*Juncus effusus* (dominant), *Anthoxanthum odoratum*, *Carex panicea*, *Equisetum fluviatile*, *Eriophorum polystachion* and *E. vaginatum*,

TEXT-FIG. 2.



Juncus supinus, *Luzula campestris*, *Menyanthes trifoliata*, *Orchis maculata*, *Potentilla Tormentilla*, *Selaginella spinulosa*, *Sparganium minimum*, *Scabiosa Succisa*, and *Viola palustris*.

Sequence of strata :—

- A. 100 cm. *Carex-Scirpus caespitosus* peat.
 B. 275 cm. A very thoroughly humified moist substance, most resembling a sort of dy.
 C. 125 cm. **Gyttja.**
 D. (at 500 cm.). **Sand.**

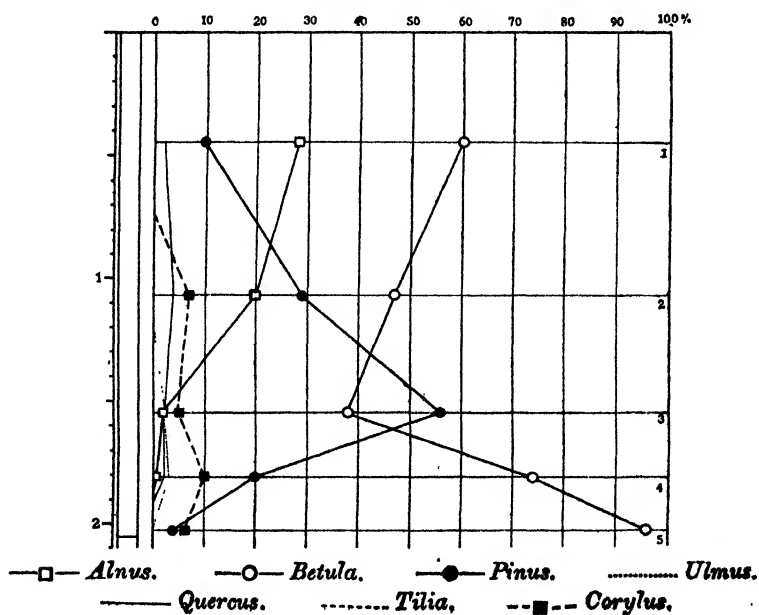
In Scotland one very seldom meets with well-defined contacts between the different kinds of peat and mud. In this peat moss, as in most others, there is a gradual passage from one kind of peat or mud to another.

If pollen-diagrams are compared with one another, the greatest caution is necessary when trying to synchronize a layer in one peat moss with a layer in another, unless the evidence is based on more than a resemblance in the form of the pollen-curves (*cf.* Erdtman, 1921, p. 24). In the present case, however, the layer from which sample 6 is taken shows so conspicuous a resemblance in its pollen-flora to the A-zone of peat moss No. 1, that they can scarcely be other than synchronous. Another resemblance lies in the fact that the PF is greatest in this layer in both peat mosses. Thus it is evident that the formation of peat in No. 1 first began when the formation of gyttja in No. 2 had ceased, and the lake which had formerly occupied the site had been silted up.

Pollen of *Tilia* occurred in sample 3, and that of *Myriophyllum alterniflorum* in the three gyttja samples (frequency small, maximum 3.3 per cent. in sample 9).

PEAT MOSS NO. 3.

TEXT-FIG. 3.

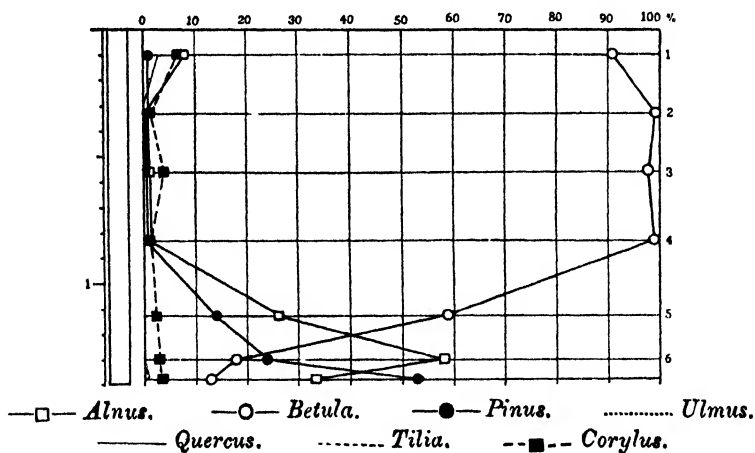


The view has been put forward that the remains of pollen-grains embedded in peat would differ from those embedded in mud (*cf.* Malmström, 1923 p. 147*). If this always were so, the reliability of the diagrams would be considerably reduced. I have already discussed this question (1921), and my opinion is that the pollen-spectra are influenced very slightly, or not at all, by the matrix in which the pollen-grains are embedded.

In order to explore this problem further, a series of samples was collected from genuine hill-peat only 200 m. from the peat moss just described (No. 2). The furrows caused by erosion reach a depth of 2 m. in this peat, and pine-stools occasionally occur. This moss seems to have originated at the same time as moss No. 2, because the pollen-spectrum of sample 5 is in accurate correspondence with the spectrum of the lowest gyttja stratum in No. 2. There seems to be no doubt as to the identity of the horizon of sample 3 (with its well-defined *Pinus*-pollen maximum) with the A-zone. At what time the formation of peat ceased cannot be stated owing to the scantiness of the material for study.

PEAT MOSS No. 4.

TEXT-FIG. 4.



Situation: A little W. of the west end of Loch a' Chroisg, 110 m. N.E. of the point of the map where the road Achnasheen-Kinlochewe crosses Allt na Fèithe Bàine; altitude above sea-level about 200 m.

This moss is quite a small one, resting on sand. The surface is clothed with a dense carpet of *Calluna*, *Erica*, *Myrica*, *Potentilla erecta*, *Scirpus*

* Malmström shows that in lake deposits the frequency of conifer pollen is considerably greater in sediments formed very near the shore than in sediments deposited in deep water. This difference might, however, be of but little importance when dealing with small, shallow lochs or mere hollows in the peat filled by water.

cæspitosus, etc. The samples were collected in an exposure, with the exception of the two lowest, which were obtained with the bore.

The 20 cm. at the top were interwoven with living rootlets; below these followed 120 cm. of birch-forest peat. The birch-remains occurred most abundantly 40–60 cm. below the surface; further down perfect leaves of birch were found.

That a local birch or alder clump (but usually not a clump of pines) has a great influence on the fossil pollen-flora has been stated over and over again, and recent investigations by the author in N.W. Germany (Geol. För. Förh. 1924) and France (départ. Finisterre) have added fresh confirmation. The moss we are speaking of is also instructive upon this point. In the stratum which showed the greatest occurrence of birch-remains there were counted: in sample 2, 236 pollen-grains (1 *Alnus*, 230 *Betula*, 2 *Pinus*; 3 *Corylus*); in sample 3, 159 (2 *Alnus*, 150 *Betula*, 1 *Pinus*; 6 *Corylus*); and in sample 4, 152 (1 *Alnus*, 148 *Betula*, 1 *Pinus*; 2 *Corylus*).

Judging by the fossil pollen-flora illustrated in the diagram, the moss would seem to be somewhat later than the A-zone of the moors already noted. In the lowest layer pine-pollen is dominant, in the next higher alder, and in the highest birch-pollen. This fact is not at all in correspondence with the general sequence of strata described by Lewis and Samuelsson.

Pollen of *Tilia* and *Polypodium* spores were obtained from sample 7.

PEAT MOSS No. 5. (Text-fig 5.)

Situated in the neighbourhood of Strathcarron, E. of R. Carron and N.W. of the upper end of the fjord-like Loch Carron, 600 m. E. of the letter "O" in New Kelso. The moss lies at the 50-foot raised beach (about 14 m. above sea-level). This moss has the character of a high moss with a gently-sloping surface. A layer of pine-stools immediately overlies the basal sand. The surface vegetation consists of an *Erica cinerea*-*Scirpus cæspitosus* association with *Calluna*, *Myrica*, and *Narthecium*; subordinately, *Eriophorum vaginatum*, *Drosera longifolia*, *Pinguicula vulgaris*, and *Menyanthes trifoliata* (in wet places only) occur; sphagnids, lichenids, and eubryids (terms from Du Rietz, 1921) are very scanty. The little tarn in the northern part of the moss, south of the terminal moraine, rests directly on sand; no gytja is formed.

Sequence of strata:—

- A. 20 cm. Well humified, dry, humus-like substance.
- B. 30 cm. *Eriophorum vaginatum* peat, black; H = 6*.
- C. 47 cm. Do., brown, turning black in the air; H = 6–8.

* H=degree of humification, according to von Post's scale of ten divisions, 10 being the highest. Cf. von Post, 1920 (cited in German in Erdtman, 1921, p. 55).

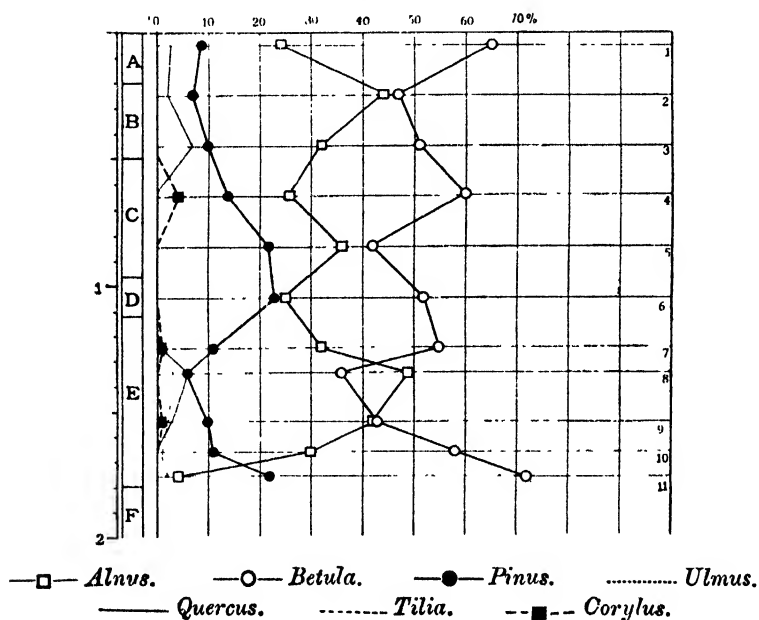
D. 15 cm. *Sphagnum* peat, bright brown, with a considerable number of large *Calluna* stems ; H = 5.

E. 68 cm. Pine-moss peat, H = (7-)8 : stools of pine.

F. (at 83 cm.) **Sand.**

The glen in which this moss is situated stretches from Achnashellach, near Loch Dùghaill to Loch Carron, and Attadale. The vegetation is here of a very different character from that of the high mountain district between Glencarron over Achmasheen to Acharralt. On the hillsides the forests, chiefly of birch and oak, attain a size but seldom met with in North Scotland. This fact must be taken into account when interpreting the pollen-diagram, which in some respects clearly differs from the diagrams so far described.

TEXT-FIG. 5.



The most salient feature is the great frequency of alder-pollen, which, for instance, in sample 8 forms one-half of the total tree-pollen (cf. p. 459, the alder-pollen maximum in No. 2, which is only 14 per cent.). It is probable that alder has played an important part in the composition of the forests which formerly surrounded Loch Carron at the time of the last fall and rise of the land. In a moss in S.W. Sweden (Erdtman, 1921, diagram 21, plate 8), two alder-pollen maxima occur: one in a stratum immediately above, another in a stratum immediately below, an intercalated bed of marine origin (Tapes Sea, *Litorina* subsidence).

The lowest layer of this moss is probably synchronous with the A-zone (pine-stools, low frequency of alder-pollen), in which case the layer with the greatest amount of *Alnus* pollen would best correspond with that from which sample 6, moss No. 4, was taken.

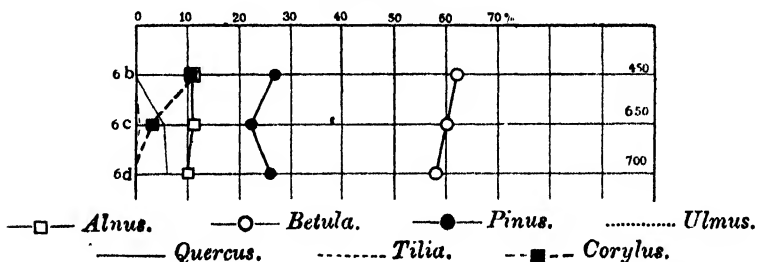
Pollen of *Chenopodiaceae*, which is frequently met with in mosses near the sea (cf. Erdtman, 1921, p. 135; Halden, 1922), is recorded from sample 11, guard-cells from the stomata of pine needles from samples 9–11.

Some Observations from Smaller Peat-deposits.

PEAT MOSSES NOS. 6 a, b, c, d. (Text-fig. 6.)

From the hillsides around Loch a' Chroisg, N.W. of Lubmore and about 265 m. above sea-level, a series of samples was taken from a bog with *Carex rostrata*, *Eriophorum polystachion*, *Juncus supinus*, *Narthecium ossifragum*, *Pinguicula vulgaris*, *Potamogeton polygonifolius*, etc. The peat varied in thickness from 150–200 cm. A sample taken immediately above the rocky bed of the bog, when analysed, showed the following percentages: *Alnus*, sporadic (1.3), *Betula*, 98 (98), *Pinus*, 2 (0.7); "*Corylus*," 2.8 (4). The figures in brackets are taken from sample 3, moss No. 4, and are given for comparison. Of course these samples are synchronous, and, if so, this bog must be considerably later than the peat-deposits described above.

TEXT-FIG. 6.



The diagram (fig. 6) shows three pollen-spectra from the hills N. and N.W. of Achnasheen. 6b was collected about 10 m. N.E. of Allt Achad na Sine, 450 m. above sea-level; 6c about 550 m. N.W. of the point 2101 at the name "Creagan nan Laogh" (650 m. above sea-level), and 6d on "Sail" and Tuim Bhain (about 400 m. W. of "S" in "Sail," and 700 m. above sea-level). The samples are taken from the bases of mounds of peat, the relics of the shallow bed of peat which once covered the whole slope. Their pollen character seems best to correspond with a zone somewhat younger than the A-zone (cf. sample 5, moss No. 1, and sample 5, moss No. 2). In sample 6c there occurred a single lime pollen-grain. No specimens were taken from a greater altitude than these, but the presence of pollen-grains alone is not sufficient evidence on which to arrive at a definite conclusion with regard to the vertical distribution of trees.

B. *Peat Mosses on the Isle of Skye.*

PEAT MOSS No. 7. (Text-fig. 7.)

Situation : N.N.W. of Sligachan between Allt Dubh and the point $8\frac{1}{2}$ of the Sligachan-Portree road. Altitude about 65 m. above sea-level.

The samples 1-3 were taken in an exposure made by peat-cutters, the others with the bore.

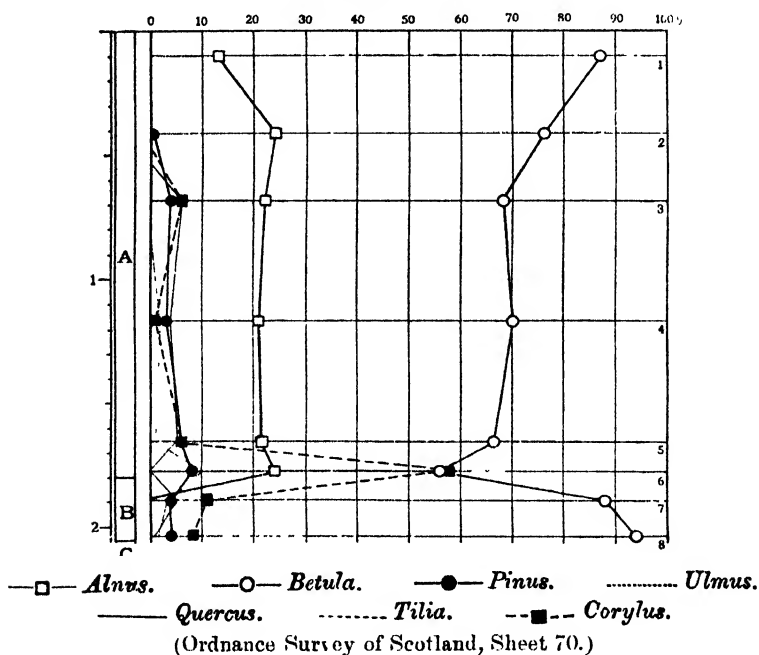
Sequence of layers :—

A. 180 cm. *Eriophorum vaginatum* peat, well humified, especially below (H=8-9), brown-black.

B. 25 cm. **Mud** resting on

C. (at 205 cm.) **Gravel.**

TEXT-FIG 7.



Sample 6 shows a remarkably high *Corylus* percentage, the frequency being a little greater than that of *Betula* (58, resp. 56 per cent.). *Tilia* pollen was recorded in sample 6.

PEAT MOSS No. 8. (Text-fig. 8.)

Situation about 1500 m. N.W.-W.N.W. of Sligachan at the southern end of Loch nan Eilean. Altitude above sea-level about 76 m.

In the loch there grew, amongst other plants, *Lobelia Dortmanna*, *Potamogeton polygonifolius*, and *Sclerurus nigricans*, and on the wet meadow, from which the borings were taken, *Drosera longifolia*, *Menyanthes*, *Myrica*,

Pinguicula vulgaris, *Scirpus cespitosus*, *Platanthera bifolia*, *Silene nigrans*, *Selaginella spinulosa*, *Sphagnum*, and *Amblystegium* spp.

Sequence :—

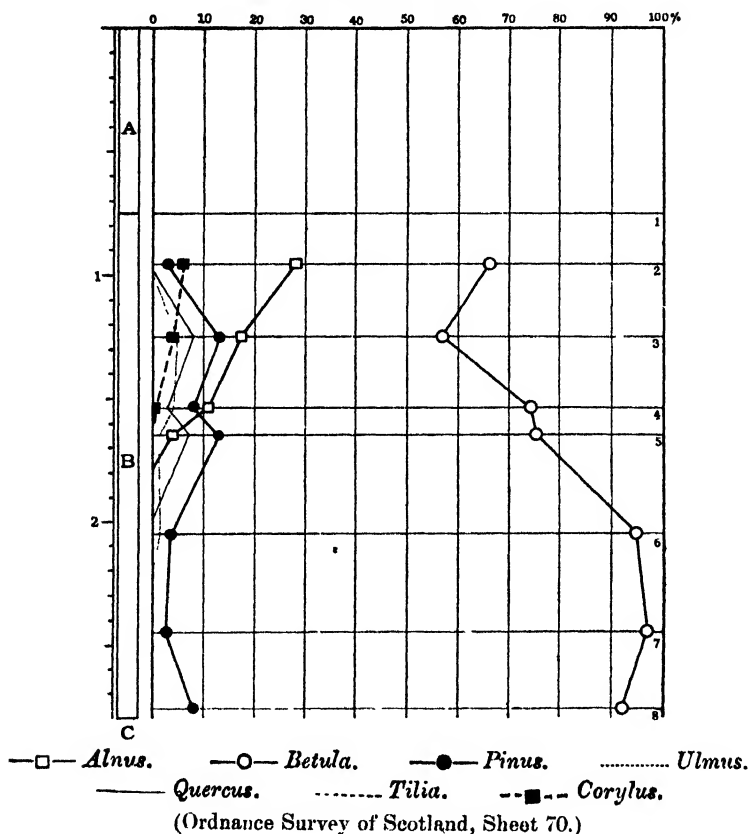
A. 75 cm. *Carex* peat.

B. 205 cm. *Gyttja* (in the oldest layers a typical *Epithemia gyttja*).

Between 46 and 92 cm. below the surface was a layer with a considerable amount of very fine sand.

C. (at 280 cm.) Rock.

TEXT-FIG. 8.



Myriophyllum alterniflorum pollen occurred in sample 6, *Nuphar* in 3, 4, *Nymphaea* in 2, 5, 6, 7, etc.

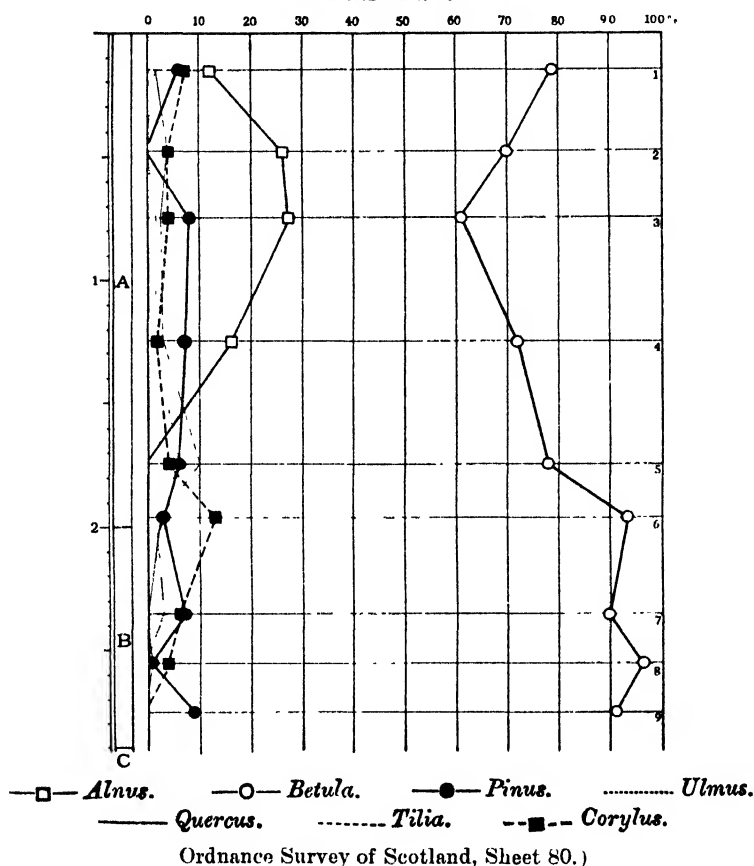
PEAT MOSS No. 9. (Text-fig. 9.)

Situated at a low altitude above sea, N.W. of Portree, in a wide expanse of slightly undulating moorland. On the surface grew *Calluna*, *Drosera longifolia*, *Erica cinerea*, *Eriophorum vaginatum*, *Molinia caerulea*, *Narthecium*, *Polygala*, *Potentilla Tormentilla*, *Scirpus cespitosus*, *Rhacomitrium lanuginosum*, etc.

The beds are as follows :—

- A. 200 cm. *Sphagnum* peat, closely intermingled with *Eriophorum vaginatum* remains ; lowest dark brown, H 8–9, forming a transition to
 B. 90 cm. Peat, most resembling *Carex* peat, very compressed and difficult to force with the bore ; seeds of *Menyanthes*.
 C. (at 290 cm.) Green sand.

TEXT-FIG. 9.



Lewis (ii. 1906, p. 338) studied exactly the same moss, and he, too, remarks that the layers are not well-defined. In the lowest layer he saw twigs of *Betula alba*.

The three diagrams from Skye (text-figs. 7, 8, and 9) agree chiefly in three respects: 1, the dominance of birch-pollen in the oldest layers: 2, the sudden appearance of alder-pollen, which very soon attains a great frequency: 3, the low frequency of pine-pollen.

In Part II. p. 353, Lewis says: "No trace of Arctic plants has hitherto been found either at the base or elsewhere in the Hebridean peat, thus

showing that there is a break of continuity between the glacial deposits and the peat that rests upon them." There is nothing in the diagrams from Skye to contradict this supposition. Further down on the same page Lewis continues: "The character of the basal layers of peat would seem to indicate more genial and drier conditions than obtain at present; for the greater part of Skye and North Uist (about 75 per cent. in one and 90 per cent. in the other) now covered with peat was clothed with thick woods of birch and hazel, with some alder. Such a type of vegetation is hardly represented in the islands at the present day. Allowance must, however, be made for the fact that when this woodland period existed the peat was extremely thin and presumably better drained than now."

As *Alnus* pollen does not occur in the oldest layers, the alder wood, which is sometimes found there, is presumably the remains of the roots of trees, which at a later time grew on the boggy ground. There seems no reason to suppose as Lewis suggests (*l. c.* p. 340) that there would be a break in continuity between the upper and lower part of the wood-bearing stratum in the lower part of the peat mosses. Lewis describes abundance of *Corylus Avellana* (wood, bark, nuts) from Skye, and it is extremely interesting that pollen researches in Bohemia (Rudolf and Firbas, 1923), Scotland, and Sweden (von Post, 1920), show a maximum frequency of hazel-pollen in relatively early postglacial beds. In Skye, however, the hazel copses of this period seem to have had a rather local distribution. Sample 6 in No. 7 (with 58 per cent. *Corylus* pollen) shows the greatest pine-pollen frequency in this moss, and may perhaps be synchronous with the A-zone. The same may be said of sample 5, No. 8.

C. Peat Mosses on the Island of Lewis.

(Map used: Bartholomew's "Half-inch to mile" map of Scotland, Sheet 23.)

According to Lewis (III. 1907, pp. 47-48) the Lower Forest in this island usually consists of a thick bed of birch, fairly large trees, mixed, in some places, with *Corylus avellana* and *Alnus glutinosa*. The bed often exhibits features which indicate that rapid denudation was going on during its formation. The upper layers of peat contain no trace of forest, thick beds of *Scirpus* and *Eriophorum vaginatum* peat lying at the Upper Forest horizon instead of *Pinus silvestris*.

According to Samuelsson (*l. c.* p. 215) a section close to the road, about 4 km. south of Barvas, showed the following strata:—

- A. 200 cm. of *Eriophorum vaginatum* peat, also containing *Scirpus caespitosus* remains, not decayed and entirely without any remains of trees, but with solitary *Calluna* stems.
- B. 25 cm. do., highly decayed, very rich in trunks and twigs of birch and heather.
- C. 50 cm. do., with solitary remains of dwarf shrubs.

D. 10 cm. do., with numerous *Empetrum* stems.

E. 25 cm. do., with numerous birch branches and twigs of at least as large a size as those found in the upper forest bed.

F. Moraine.

From this section Samuelsson concludes that the district has twice been covered by a birch forest, which has been replaced by more hydrophilous associations, and he suggests that the forest-remains found by Lewis belong to the Upper Forest. That Lewis nowhere found any analogy to the Lower Forest may, in Samuelsson's opinion, possibly depend upon the character of the oldest strata (lake deposits) at the point where he found the most complete stratification.

Upon the island of Lewis I have studied (in sections and with the bore) 20 peat deposits of different kinds, ranging in depth from 100 to 520 cm. The combined thickness of all the strata investigated may be about 40 m. In these deposits tree-remains have been met with but seldom, and in most cases the deposits seem to have originated in boggy ground. The lack of more detailed investigations makes it impossible to parallel, as Samuelsson does, the two birch layers with the Upper and Lower Forest beds respectively; and it seems equally impossible to state whether the birch stratum described by Lewis corresponds with the upper or with the lower layer found by Samuelsson. The statistical method of pollen research often shows the untenableness of such over-hasty parallelisms, the pollen-curves in a forest-bed of a certain moss being almost the same as those (*e.g.* in a layer of *Sphagnum* or *Amblystegium* peat) in another, although in the latter there are perhaps two forest-beds lying, the one above, and the other below the more hydrophilous stratum.

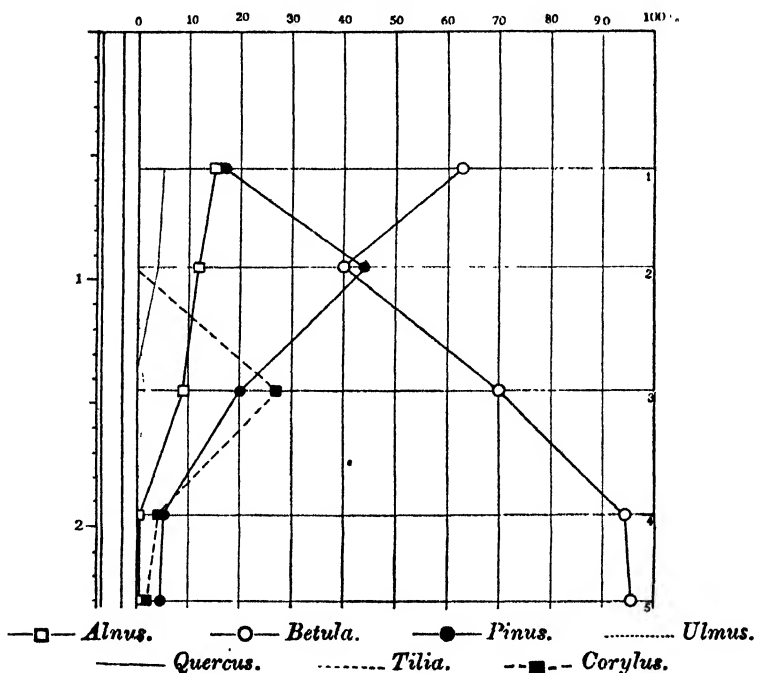
The stratification of peat or mud (gyttja) deposits often furnishes the most decisive proof as to changes in postglacial climate. From the deposits of Middle Europe, Gams and Nordhagen (1923) have furnished a valuable contribution to the criteria for estimating such changes. In some countries, however, either peculiar topography (Finland; *cf.* Auer, 1923) or the influence of unremitting climatic factors (Scotland, or at least parts of it) may have been of such importance that local edaphic factors have given their stamp to the deposits, or have to a certain extent prevented them from showing those characters which would have been theirs if the general climatic conditions had been able to exercise an undisturbed influence upon their development. The importance of edaphic factors has been accentuated by many authors; most recently by Salisbury (1921 & '22). On the other hand, Gams and Nordhagen (*l.c.*) consider that there have been further climatic changes (*e.g.* during the subatlantic time there must have been at least one drier period), and Gerassimoff (1923) suggests that the alternation of many thin pine-trunk layers with strips of slightly decayed *Sphagnum*, as described by him from the peat moss of Galitz (Tver), may be due to slight changes of climate.

PEAT MOSS No. 10. (Text-fig. 10.)

Situated 60 m. N.E. of Sandwick Loch, E. of Stornoway. The thickness of the strata is 233 cm. It consists of *Carex* peat, in the upper part resembling magnocaricetum peat ($H=8$), further down containing *Menyanthes* seeds and *Equisetum* remains, also rhizomes of *Phragmites*. The base shows a transition to a dark, very much decayed muddy substance resting on rock.

As to the diagram (text-fig. 10), sample 3 shows an unusually well-defined maximum of *Corylus* pollen; consequently this sample seems to be synchronous with the A-niveau, the frequency of alder-pollen still being rather low.

TEXT-FIG. 10.



It is remarkable that in one sample (2) pine-pollen is the dominant (44 per cent.). Such high percentages are not met with in western Lewis. However, this figure is not well established, for only 25 pollen-grains were counted. Pollen of *Myriophyllum alterniflorum* is recorded from sample 4.

On the seashore S. of Sandwick Loch and a little above the mean high-water level, there are two strips of peat, the lower (15 cm. thick) resting on shore-gravel and separated by 10 cm. of gravel from the upper (10 cm. thick), which is itself covered by 10 cm. of gravel. It cannot be doubted that these peat-layers have the same history as those described by Samuelsson (*l. c.* p. 244) from the bay between Rudha Shilldinish and Gob Shilldinish, south-east of Stornoway. From Sandwick Bay, Lewis (*iii.* 1907, p. 49)

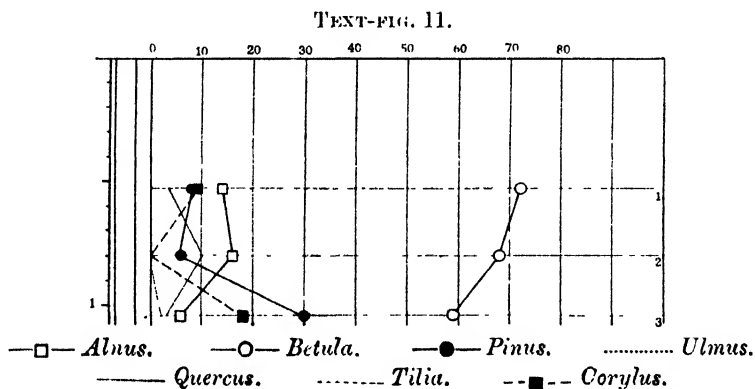
mentions the presence of submerged peat, and Mr. D. Mackenzie, of Stornoway, has kindly told me that such peat also occurs at the new quay of Stornoway Harbour and in the wick S.W. of Arnish Point (N. of Tob Leirabhaidh).

Unfortunately, whilst I was in Lewis, the tides were not low enough to permit of sections being cut. By analysing samples of submerged peat we should get a number of fixed points much more useful for purposes of correlation than many forest-beds.

PEAT MOSS No. 11. (Text-fig. 11.)

Situated S.W. of Steinish, between the Steinish road and the little stream west of it. A shallow deposit (108 cm.) resting on sand; the surface covered with a firm grass meadow with *Anthoxanthum*, *Juncus effusus*, *Nardus*, *Trifolium repens*, *Viola palustris*, etc.

The lowest sample, which showed fragments of Spongiae needles, spores of *Polypodium vulgare*, and pollen of *Epilobium*, has a high frequency of pine- and hazel-pollen and a low one of alder; it thus exhibits the main features



of the A-zone. The 3 samples analysed showed a high frequency of *Salix* pollen (in sample 1, 50 per cent.; 2, 150 per cent.; 3, 75 per cent.), which, however, must not be regarded as a proof of a colder climate, because local willow-clumps along the stream or the sea-shore could well have caused this high pollen-frequency. In Lewis it is to be remarked there is a considerable difference between the PF of the younger layers and that of the older. This fact and its great theoretical importance with regard to the statistical method of pollen research is dealt with in another paper (Erdtman, 1924), to which I beg to refer.

PEAT MOSSES Nos. 12 a and b.

The former is situated on the sea-shore between Steinish and the mouth of the stream west of it. The deposit is certainly decapitated, the surface being clothed with *Ulex europaeus*, *Pedicularis silvatica*, *Eriophorum polystachion*, *Potentilla Tormentilla*, etc.

The latter is a deposit 40 cm. above mean high-water level, immediately south of the mouth of the River Laxdale. It is covered by a saline meadow showing *Armeria*, *Festuca rubra*, *Glaux*, *Juncus Gerardi*, and *Plantago maritima*.

The thickness of the peat is, in 12 *a*, 146 cm., in 12 *b*, 110 cm. At a depth of 112 to 114 cm. below the surface in the former, and 67 to 68 cm. in the latter, there runs a continuous layer of sand. The peat immediately above and below this layer contains numerous small sand-grains, which make the analyses very troublesome. In a sample from 11 *a*, 95 cm. below the surface, there were counted: 1 *Alnus* pollen-grain, 2 *Betula*, 2 *Pinus*, 1 *Quercus*; and in a sample 125 cm. below the surface, 10 *Betula*, 5 *Pinus*, and 3 *Corylus* pollen-grains. A sample from 11 *b*, above the sand-strip (47 cm. below the surface), showed: *Alnus* 16 per cent., *Betula* 69 per cent., *Pinus* 2 per cent., *Quercus* 13 per cent.; *Corylus* 7 per cent. [also pollen of *Myriophyllum alterniflorum* (sporadic) and a *Chenopodiaceae*]; and a sample from below the strip, 80 cm. below the surface: *Alnus* 16 per cent., *Betula* 68 per cent., *Pinus* 4 per cent., *Ulmus* 12 per cent., and *Corylus* 16 per cent. In both deposits the pine and hazel percentage are greatest in the lowest samples, which gives a hint that they are approximately of the age of the A-zone. Probably the sand-layer in the one moss is synchronous with that in the other.

PEAT MOSS No. 13.

Situated north of Stornoway at the S.W. point of a little tarn, the water of which flows north-east to Allt an-t Snìomh and thence to Broad Bay (Loch a Tuath). The level of the pool is about 65 cm. lower than the point where the boring was made.

Sequence:—

A. 100 cm. *Sphagnum* peat mixed with *Scirpus* and *Calluna* remains; H=6-7.

B. 100 cm. Do., almost typical; H=4.

C. 140 cm. Do., H>6; black below, containing small twigs.

A sample taken 5 cm. above the basal sand showed: *Alnus* 2 per cent., *Betula* 88.25 per cent., *Pinus* 9 per cent., *Quercus* 0.75 per cent.; *Corylus* 18 per cent.; cf. *Salix* 10 per cent.

PEAT MOSS No. 14.

Situated 75 m. east-north-east of No. 13. A boring was made on the margin of a little loch, and showed a sequence, 130 cm. thick, resting on rock. A sample 3 cm. above the ground contained: *Alnus* 12 per cent., *Betula* 53 per cent., *Pinus* 32 per cent., *Quercus* 3 per cent.; *Corylus* 9 per cent. Because of the greater alder- and oak-pollen frequency and the smaller frequency of hazel-pollen, this sample seems to be a little younger than that from moss No. 13.

North of Stornoway much peat is cut for fuel. Although in places the peat in the Isle of Lewis is wasting, places are also to be found where plants

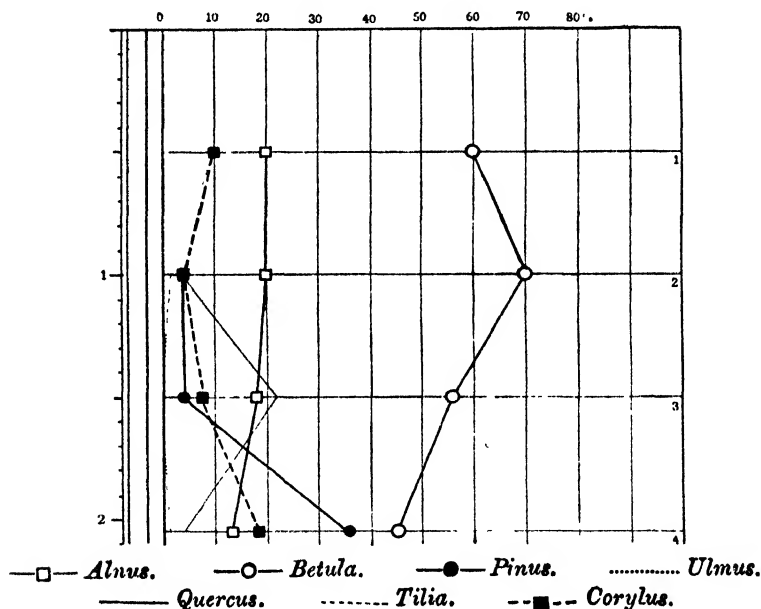
invade the old water-logged cuttings, in the end forming new peat. In the neighbourhood of moss No. 14 five stages of succession were seen :—

1. *Menyanthes*.
2. *Menyanthes*, *Sphagnum*.
3. *Menyanthes*, *Sphagnum*, *Juncus supinus*, *Eriophorum polystachion*, *Scirpus uniglumis*.
4. *Calluna*, *Sphagnum*, *Erica Tetralix*, *Drosera rotundifolia*, *Potentilla Tormentilla*, *Molinia caerulea*.
5. *Calluna-Rhacomitrium* heath.

PEAT MOSS No. 15. (Text-fig. 12.)

A boring was made at the south-east margin of a tarn S.W. of Stornoway, immediately east of the Stornoway-Loch Chlathamir-Crossbost road and N.N.W. of the point where this road crosses Allt na Craoibhe. No

TEXT-FIG. 12.

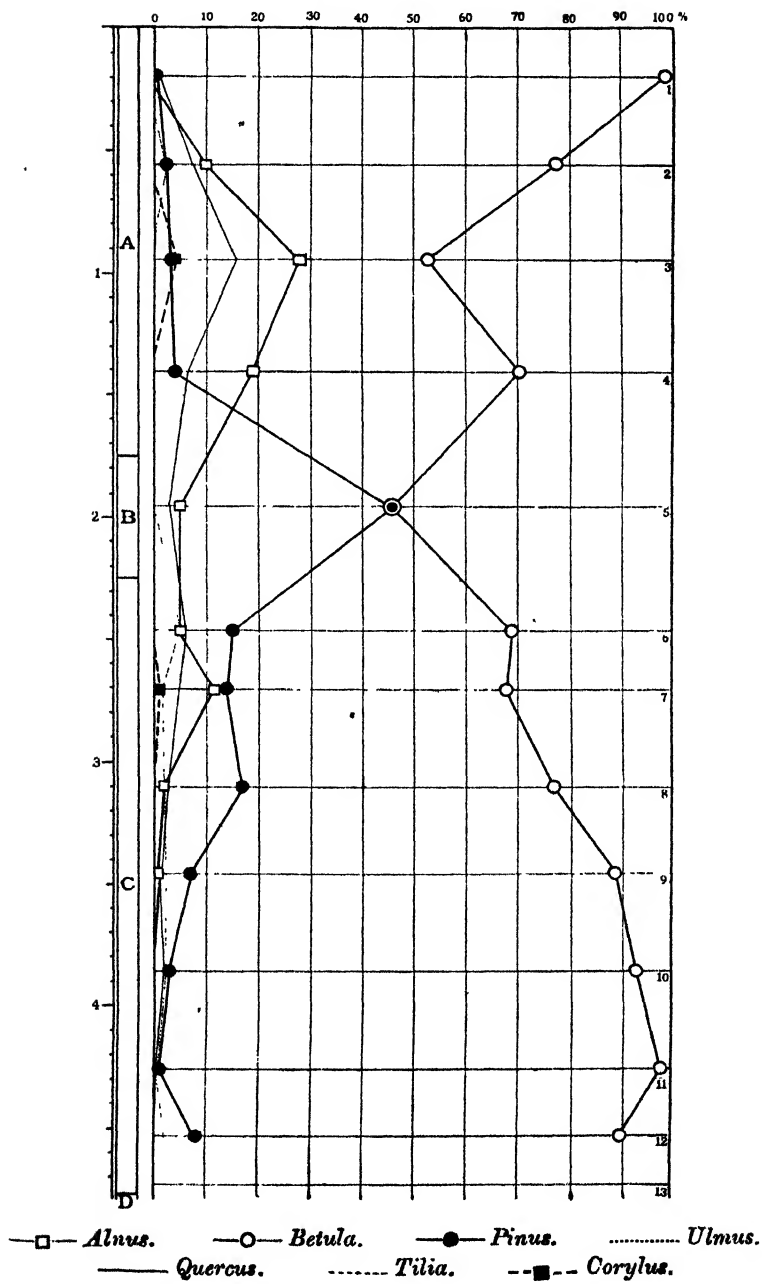


phanerogamous plants grew in the loch, though fossil *Nymphaea* pollen was found. The margin of the loch was bordered by widespread *Calluneta* with *Drosera rotundifolia*, *Erica Tetralix*, *Eriophorum vaginatum*, *Potentilla Tormentilla*, *Scirpus caespitosus*, *Rhacomitrium lanuginosum*, etc.

The thickness of the peat was 210 cm. It consisted to a great extent of much decayed *Sphagnum* peat with some thin layers of wetter peat (resembling *Carex* peat; 120 cm. beneath the surface a seed of *Menyanthes* was found). The level of the loch was 135 cm. lower than the point where the boring was taken. The pollen-spectrum of the lowest sample (No. 4) is that of the A-zone or a stratum somewhat younger than it.

PEAT MOSS No. 16.

TEXT-FIG. 13.



A boring was made east of moss No. 15 at the western point of the little loch to which the water from Loch Mor a' Ghriàinain and L. Mor a' Chrolaich drains before it flows to Allt na Craoibhe. In the loch was a very sparse flora (*Carex rostrata*, *Menyanthes*, *Potamogeton*, etc.).

Sequence :—

- A. 175 cm. *Sphagnum* peat; not at all a typical one; fairly rich in Ericaceæ remains.
- B. 50 cm. of a substance resembling a *Carex* peat, forming a transition to
- C. 252 cm. gyttja, of which the colour ranges from dark brown to yellow-green.
- D. 3 cm. + clay, sandy.

The layer A has a low PF; Ericaceæ tetrads, however, are common; for instance, in sample 3, where they form 300 per cent. of the total pollen. Layer B and, in a higher degree, layer C are rich in pollen, except the lowest samples from C. [In sample 13 only 18 pollen-grains were counted: 9 *Betula*, 9 *Pinus*. *Myriophyllum alterniflorum* pollen occurred here with a frequency of 112 per cent. It is curious that this pollen was found also in sample 5 (sporadic) and 6 (16 per cent.).]

The diagram differs considerably from the diagrams already mentioned; it is noteworthy that *Corylus* pollen is almost absent. Undoubtedly pollen masses from local birch forests have considerably influenced the pollen-flora (cf. samples 9–12), and it therefore seems difficult to localize the A-zone. Sample 5 shows a great pine-pollen percentage, but it is more probable that the layer from which sample 8 was obtained originated at the time of the A-zone. The presence of pine-pollen in all samples from this deep deposit does not favour the view that pine did not grow in Scotland before the Upper Forest time.

PEAT MOSS No. 17.

Situated W. of Stornoway and S. of Loch Garbhaig, N. of the old road to the north of Amhuinn a' Ghlinne Mhoir, a little N.W. of point 250.

Beneath 263 cm. of peat with *Sphagnum*, *Carex*, and *Scirpus cespitosus* remains, there follows a gyttja bed, 32 cm. thick, resting on sand. From the gyttja layer pollen-grains are practically absent, the analysis of a sample taken 15 cm. above the sand showing only a single pollen-grain (birch). A sample from the peat 255 cm. beneath the surface gave the following results: *Betula* 92 per cent., *Pinus* 6 per cent., *Quercus* 1 per cent., *Ulmus* 1 per cent.; *Corylus* 3·5 per cent.

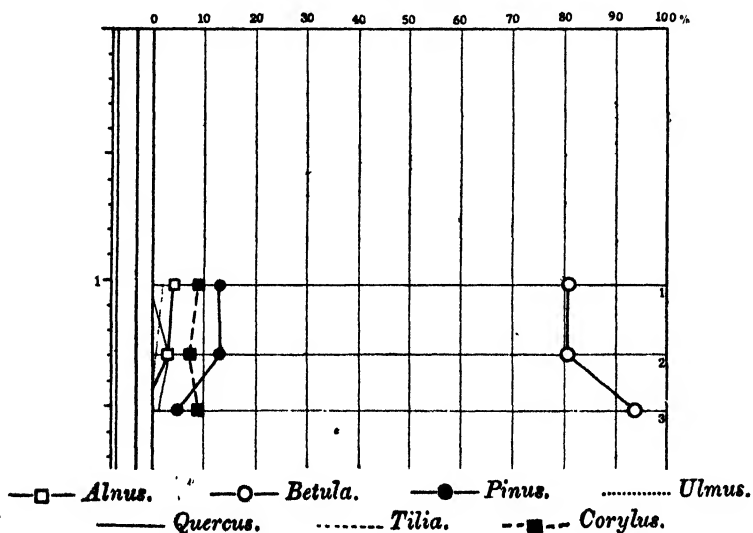
PEAT MOSS No. 18.

Situated on the W. coast of Lewis, near East Loch Roag, beside the road a little N. of Breascleif. The sequence is 170 cm. thick. In the oldest layers, which rest on rock, only 1 *Acer*, 12 *Betula*, 1 *Pinus* (1 *Quercus*?), and 2 *Myriophyllum alterniflorum* pollen were met with. Also 2 spores of *Polypodium vulgare*, pollen of Cyperaceæ and Gramineæ, *Pediastrum* sp., and Ostracod remains were recorded.

PEAT MOSS No. 19. (Text-fig. 14.)

On the seashore at Callernish, S.W. of Loch Bhàrrabhat, a number of turfy mounds are to be found scored by great crevices, the result of desiccation. The thickness of these mounds is about 175 cm., and their base is regularly washed by the tide at high water. The pollen-character shows these deposits to be a little older than the A-zone. If this synchronization could be established by further investigations, and if the A-zone really is a part of the Lower Forest, these peat deposits would be of importance for solving the problem of the rise and fall of land in the Outer Hebrides. Parts of eastern Lewis were submerged in postglacial times, but possibly

TEXT-FIG. 14.



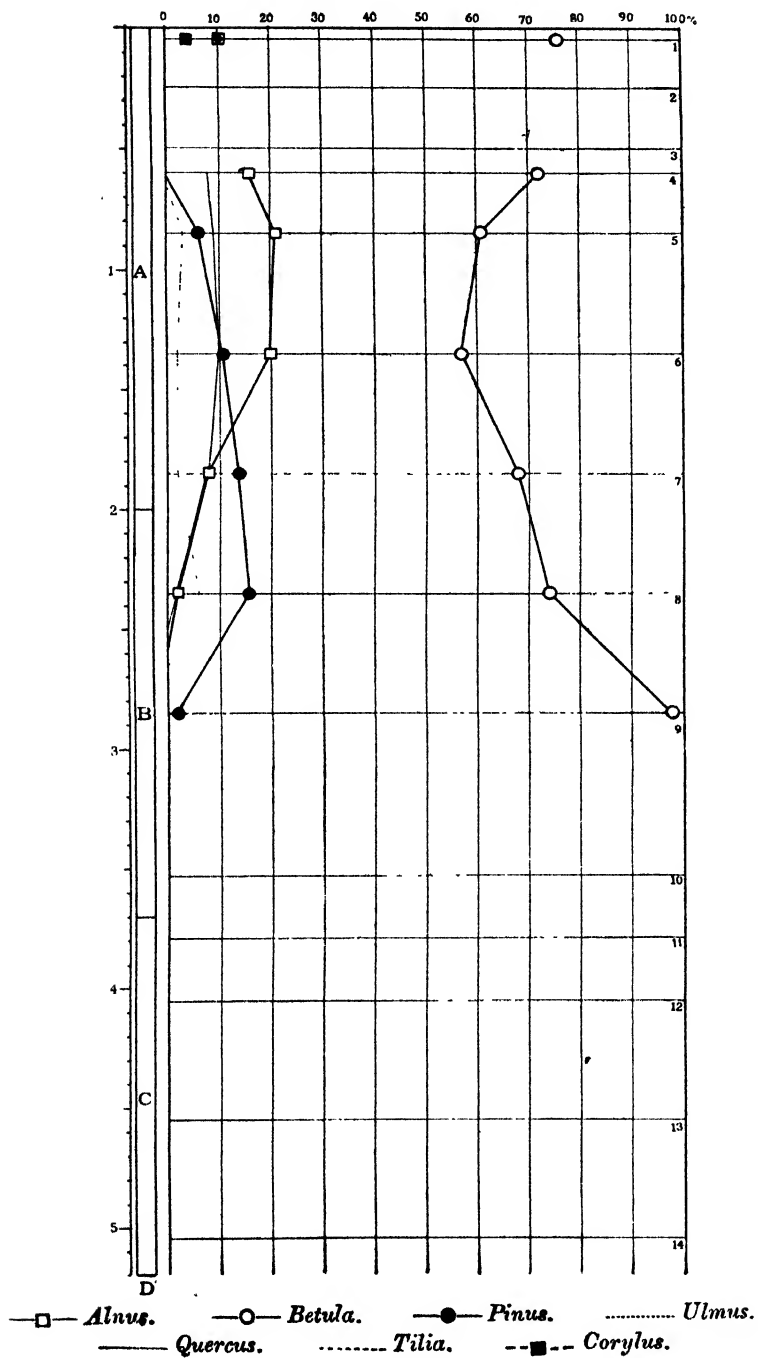
the western part was not. *Sphagnum* remains are quite common in the peat, and it is obvious that the "*Salix*" percentage is greater than usual (sample 3, 9 per cent. ; 2, 13 per cent. ; 1, 30 per cent.).

PEAT MOSS No. 20.

Situated on the west coast of Lewis, on the right bank of the River Arnol, between Loch Arnol and the Barvas-Carloway road. Vegetation: a firm meadow with *Anthoxanthum*, *Festuca ovina*, *Pedicularis silvatica*, *Plantago maritima*, etc. Samples were not collected at a greater depth than 160 cm. below the surface. It was possible to analyse a specimen from that depth, in spite of its great content of sand-grains; it showed the following pollen-spectrum: *Alnus* 15 per cent., *Betula* 85 per cent.; *Corylus* 2.5 per cent.; "*Salix*" 15 per cent.; *Myriophyllum alterniflorum* 5 per cent.

PEAT MOSS No. 21.

TEXT-FIG. 15.



Situated due S. of the road to the south of South Shawbost, about 35 m. above sea-level. A boring was made in the centre of this interesting moss, which fills a large hollow between the surrounding hills and, with its flat surface, very closely resembles a meadow.

The sequence was as follows :—

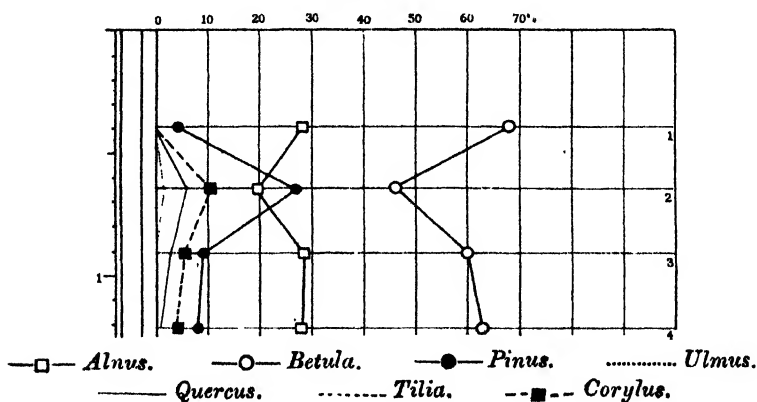
- A. 200 cm. *Carex-Scirpus caespitosus* peat.
- B. 170 cm. of a substance with a great content of **dy**; the lowest part somewhat resembling *Phragmites* peat and containing remains of *Equisetum*. It forms a gradual transition to
- C. 150 cm. **Gyttja**; yellow, but at the base greyer.
- D. 40 cm. + **clay**; grey, tough.

The diagram shows a normal alder-pollen curve; near the lowest part pine-pollen reaches a maximum. This, of course, indicates that it is the A-zone (sample 8). Lower down the pollen-grains of trees are met with but very rarely: in sample 10, 1 pine, 9 birch; sample 11, 2 birch; sample 12, 1 birch; sample 13, 1 willow; sample 14, 1 willow. Instead, the pollen of *Myriophyllum alterniflorum* is dominant in these samples ("5500 per cent." in sample 12); in sample 4 it was also seen, but only sporadically. *Ilex* pollen occurred in sample 2, beech-pollen in sample 4, and spores of *Polypodium vulgare* in most of the samples. Also in the Krutzelried at Schwerzenbach east of Zürich there are very old lime and detritus gyttjas, also without a trace of tree-pollen (Neuweiler, 1910; Gams and Nordhagen, 1923).

D. Peat Mosses at Helmsdale, Sutherlandshire.

PEAT MOSSES Nos. 22 and 23.

TEXT-FIG. 16.



Owing to bad weather, only a few observations could be made. Two series (mosses Nos. 22 and 23) were taken on the slopes of Bein Meillich west of Helmsdale, on the eastern coast of Sutherland, from rather small deposits where erosion had cut furrows, in places down to the underlying ground.

Calluna was the dominant plant, then followed *Empetrum*, *Erica Tetralix*, *Juncus squarrosus*, *Potentilla Tormentilla*, etc.

Text-figure 16 (No. 22) shows that the formation of peat began considerably later than the period represented by the A-zone, already mentioned many times. The lower half of the sequence is richer in pollen-grains than the upper. On an average there are 51 pollen-grains per sq. cm., exactly the same number as from the samples of sedentary material from Skye (*cf.* p. 465).

In moss No. 23 (300 m. from No. 22) a series was collected from a peat-pillar about 75 cm. high, which had been isolated by erosion. The formation of peat probably began here at about the same time as in No. 22, as indicated by the analysis of the lowest sample: *Alnus* 29 per cent., *Betula* 47 per cent., *Pinus* 20 per cent., *Quercus* 3.2 per cent., *Tilia* 0.8 per cent.; *Corylus* 4 per cent.

E. Peat Mosses on the Orkney Islands.

(Map used: Bartholomew's "Half-inch to mile" map of Scotland, Sheet 28.)

The Orkneys are not nearly so rich in peat as are the Hebrides or Shetlands; nevertheless they show several points of interest, especially when the Shetland Isles are compared with the nearest part of the Scottish mainland (Caithness; neighbourhood of Cape Wrath). Lewis has published no descriptions of peat deposits from these islands.

PEAT MOSS No. 24.

This moss may be cited as an example of the distinct regenerative structure (*cf.* Sernander, 1910) sometimes met with in *Sphagnum* peat in Scotland. It is situated S.S.E. of Kirkwall, half-way between White Moss and Mark Stone Moss, about 60 m. above sea-level. The surface was clothed with a *Callunetum*. Solitary *Rumex Acetosella* also occurred.

Sequence of layers:—

- A. 21 cm. *Calluna* peat, dark and dry; a large number of *Calluna* stems and rootlets; no fibres of *Eriophorum vaginatum*.
- B. 3 cm. *Sphagnum* peat, bright brown, H < 6; rootlets and fibres of *E. vaginatum*.
- C. 4 cm. Peat, closely resembling layer A.
- D. 5 cm. *Eriophorum vaginatum* peat; no distinct boundary between this and
- E. 3 cm. *Sphagnum* peat (as B).
- F. 5 cm. Do., but dark, well humified.
- G. 6 cm. Do., bright, only a little decayed.
- H. 8 cm. Do., with a great quantity of very robust *Calluna* stems.

- I. 4 cm. *Sphagnum* peat, bright, but little decayed; fibres and rootlets of *E. vaginatum*.
- J. 6 cm. Do., dark, greatly decayed.
- K. 2 cm. Do., bright, H < 6.
- L. 10. cm. Do., brown; rootlets of *E. vaginatum*, scattered *Calluna* stems.
- M. 3 cm. Do., but brighter.
- N. 27 cm. Do., dark, but H nevertheless < 6; isolated small *Calluna* stems; *Eriophorum vaginatum* roots abundant.
- O. 115 cm. (107–222 cm. beneath the present surface). Do., H 5–7(–8); at the top was a layer with small *Calluna* stems, not very clearly defined; at 200 cm. below the surface the bore was obstructed by solid wood; lower down fossils occurred, which indicated somewhat wetter conditions (e. g. *Equisetum* remains).
- P. 150 cm. **Dy**, becoming greyish, gyttja-like or clayey lower down.
- Q. 40 cm. + tough, grey **clay**, in places mixed with coarse sand.

The section thus shows a great number of thin strata following one another irregularly, which indicates an evolution merely depending on local edaphic factors.

From the layers A–O six samples have been analysed:—

Sample 1 (10 cm. below the surface): $\frac{1}{2}$ pine-pollen, attacked by *Rhizophidium*; then 1 Chenopodiaceæ pollen, 41 Ericaceæ tetrads, 1 *Sphagnum* spore.

Sample 2 (50 cm. below the surface): 1 *Betula*; 42 tetrads of Ericaceæ.

Sample 3 (73 cm. below the surface): 1 *Pinus*; 31 tetrads of Ericaceæ.

Sample 4 (112 cm. below the surface): 2 *Betula*; 30 tetrads of Ericaceæ.

Sample 5 (147 cm. below the surface): 1 *Alnus*, 5 *Betula*; 250 tetrads of Ericaceæ.

Sample 6 (197 cm. below the surface): 1 *Acer*, 5 *Alnus*, 11 *Betula*, 1 *Carpinus*, 1 *Pinus*; 153 tetrads of Ericaceæ.

Thus, summarized, we get a total of: 1 *Acer*, 6 *Alnus*, 19 *Betula*, 1 *Carpinus*, $2\frac{1}{2}$ *Pinus*; 547 tetrads of Ericaceæ.

As there is nothing to indicate that there was ever a larger amount of pollen in these layers, which has since decayed, it is evident that the Orkneys, when these layers were formed, were practically without forests or large clumps of forest trees. Consequently they had the same character as they have at the present day.

In the P layer no Ericaceæ pollen is found, the six analyses made giving the following result:—

Sample 7 (235 cm. below the surface): 4 *Alnus*, 7 *Betula*, 2 *Quercus*; 43 grass-pollen, 10 cf. *Salix*.

Sample 8 (260 cm.): 2 *A.*, 5 *B.*, 2 *Pinus*, 2 *Q.*, 1 cf. *Ulmus*; 55 grass-pollen, 20 cf. *Salix*; Chenopodiaceæ pollen.

Sample 9 (297 cm.): 3 *A.* (=13·5 per cent.), 13 *B.* (=59 per cent.), 5 *P.* (=23 per cent.), 1 *Q.* (=4·5 per cent.); 8 grass-pollen, 16 cf. *Salix*; Chenopodiaceæ pollen.

Sample 10 (310 cm.): 1 *A.* (?), 18 *B.*, 10 *P.*; 1 *Galium* sp.; grass- and cf. *Salix*-pollen not counted.

Sample 11 (335 cm.): 26 *B.*, 3 *P.*; 2 *Corylus*; 1 *Polypodium vulgare*; 47 spores without exospore.

Sample 12 (347 cm. below the surface): 1 *B.*, 9 *P.*; 27 cf. *Salix*; 2 *Polypodium vulgare*; 22 spores without exospore.

The solid wood found in the section proves the presence of trees, since the wood cannot have been drifted. As to the scantiness of pollen, the comparatively small area of the Orkneys is to be considered. Exact analyses for places so situated demand much time and much work. In the above figures, which, however, do not permit of percentages being calculated, it is to be noted that *Corylus* occurs only close to the bottom of the sequence. It is therefore to be inferred that evolution occurred here along almost the same lines as in the Hebrides and Shetlands. The subject will be dealt with later.

PEAT MOSS No. 25.

A rather large moss of the High Moor type, which lies west of Kirkwall (S. of Liedale, N.N.W. of Windbreck) and is drained towards the S.E. into Scapa Bay. Altitude above sea-level about 60 m. As was the case in the last-mentioned moss, the greatest part of the surface was clothed with a dense growth of a pure *Callunetum*. In places, as subordinate vegetation, *Cardamine pratensis*, *Erica cinerea*, *Narthecium*, *Schœnus nigricans*, etc. was found.

Sequence of strata :—

A. 30 cm. *Calluna* peat, dry.

B. 40 cm. *Sphagnum* peat, H 4-5.

C. 180 cm. Do., H=8, in parts rich in *Eriophorum vaginatum* remains; the lowest part somewhat resembles *Carex* peat.

D. 125 cm. Carr peat (cf. Tansley, 1911) with a great amount of dy; when the bore was at 290 cm. below the surface, methane poured out.

E. 15 cm. + clay; grey, the upper part darker than the lower.

Six samples have been analysed. The only tree-pollen seen in all these samples is that of birch. Ericaceæ tetrads were not counted.

Sample 1 (135 cm. below the surface): 3 *Alnus*, 3 *Betula*, 1 *Fagus*; 2 "*Salix*."

Sample 2 (185 cm.): 6 *Betula*, $\frac{1}{2}$ *Pinus*.

Sample 3 (235 cm.) : 1 *Betula*, 1 *Ilex*.

Sample 4 (285 cm.) : 1 *Betula*.

Sample 5 (335 cm.) : 1 *Betula*, 4½ *Pinus*, 1 *Quercus*; 14 "*Salix*."

Sample 6 (385 cm.) : 5 *Alnus*, 16 *Betula*, 4 *Pinus*, 1 *Quercus* (?); 6 "*Salix*."

PEAT MOSS No. 26.

Between Finstown and Loch Harray a boring was made in a shallow peat deposit 10 m. N. of the Finstown-Stromness Road and 200 m. W. of the Birsay Road. Altitude above sea-level about 37 m. This moss is only mentioned because of the occurrence of pine-pollen in the underlying clay (perhaps a clay-gyttja). The sequence has a thickness of 93 cm., resembles a sort of dy, and contains remains of *Carex* and *Equisetum*. The latter also occurs in the underlying grey, sandy clay. In the sample from 30 cm. beneath the surface 4 pollen-grains of birch and 1 of oak were counted; 75 cm. below the surface, 2 *Betula*, 1 *Pinus*; 48 "*Salix*." In the clayey deposit, 96 cm. below the surface, 2 pine-pollen grains were seen.

PEAT MOSS No. 27.

A rather large peat moss with a level surface, situated about 70 m. above sea-level, to the N. of Stromness, about 200 or 300 m. to the S. of the most western part of the two very small lochs which lie to the W. and S.W. of Cairston. Peat has been cut in the past, and still is much cut, for fuel. The result is that parts of the moss are filled with water, near which the following species are seen :—

Cardamine pratensis.

Epilobium palustre.

Equisetum limosum.

Galium saxatile.

Glyceria fluitans.

Hippuris vulgaris.

Hydrocotyle vulgaris.

Hypericum pulchrum.

Hypochaeris radicata.

Lychnis Flos-cuculi.

Myriophyllum alterniflorum.

Nardus stricta.

Orchis latifolia.

Parnassia palustris.

Pedicularis silvatica.

Potamogeton polygonifolius.

„ *pusillus*.

Senecio Jacobaea.

Triglochin palustre.

Sequence of strata :—

A. 110 cm. **Dy**.

B. 38 cm. **Gyttja**, the base of which is most typical; green.

C. 12 cm. **Lime gyttja**, greyish white.

D. 11 cm. **Do.**, clay-gyttja-like, blue-grey; with shells of snails.

E. 14 cm. + **sand**; grey.

A sample from 40 cm. below the surface showed: 3 alder, 16 birch, 1 hornbeam (?), 3 oak, 4½ pine, and 2 hazel pollen-grains; a sample from 85 cm. below the surface, 2 alder, 4 pine, 1 hazel pollen-grains, and

1 *Polypodium vulgare* spore. The gyttja (B) is richer in pollen: 97 birch, 1 elm, 2 pine, and 1 hazel pollen-grains being counted. Layers C and D are very poor in pollen and have not been analysed.

In the brackish water of Loch Stenness, near P.O. 27 at Waith Bridge, a stinking mat of algæ (brown, red, and green) was floating along the shore, showing that the process of putrefaction is still going on in these layers; but, even so, owing to the chemical composition of pollen-exine, we should expect that it would be able to resist decomposition. In that case we should expect to find a recent tree-pollen spectrum, formed by pollen which could have been transported by wind from a considerable distance. Two samples were collected and carefully examined, but no pollen, either of trees, shrubs, or herbs, was found.

PEAT MOSSES Nos. 28 *a* and *b*.

The slopes of Wideford Hill (225 m.) W. of Kirkwall are covered here and there with shallow peat. In a section (60 cm. deep) a little N.E. of the top, three samples were collected and analysed (28 *a*).

Sample 1 (5 cm. below the surface): 6 *Betula*; 108 Ericaceæ tetrads.

Sample 2 (30 cm. below the surface): Ericaceæ tetrads very frequent; 2 Chenopodiaceæ pollen.

Sample 3 (55 cm. below the surface): *Acer* 1 per cent., *Alnus* 26 per cent., *Betula* 49 per cent., *Pinus* 13 per cent., *Quercus* 10 per cent., *Ulmus* 1 per cent.; *Corylus* 20 per cent.; tetrads of Ericaceæ and grass-pollen were of common occurrence.

West of the top, N.W. of Smerquoy, E. of Hardhill, 40 m. above sea-level, a layer of peat (No. 28 *b*), 55 cm. thick, covered the sandy sub-soil. The pollen-spectrum of the lower sample showed: *Alnus* 17 per cent., *Betula* 60 per cent., *Pinus* 14 per cent., *Quercus* 9 per cent.; *Corylus* 12 per cent.; Ericaceæ tetrads common; a single Chenopodiaceæ pollen. Thus there is a rather close resemblance in pollen character with the bottom layer of 28 *a*.

PEAT MOSS No. 29 (Westray).

Westray lies most to the north-west of all the Orkney Islands. Peat occurs here only to a very limited extent. Eday, which is said to be fairly rich in peat (*cf.* Gunn, 1910), unfortunately could not be visited. Natural woods are absent from Westray; only in the neighbourhood of Finbo were there planted trees (*Acer*) and bushes. A wet meadow with *Eriophorum polystachion*, *Hydrocotyle*, *Ranunculus acris*, *Rumex Acetosella*, etc., was investigated. It lies between the Bay of Tuquoy and Swartmill Loch, about 1 m. above high-water mark. The section was only 87 cm. thick, consisting of 84 cm. of a dy-like substance with rhizomes, and 3 cm. clay-gyttja resting on sand.

Analyses:—

Sample 1 (25 cm. below the surface): *Alnus* 13 per cent., *Betula* 80 per cent., *Ilex* 1·4 per cent., *Pinus* 5·6 per cent.; *Corylus* 15·8 per cent.; also 10 cf. *Salix* pollen, 4 spores of *Polypodium vulgare*, spores of *Tilletia Sphagni*, etc.

Sample 2 (45 cm. below the surface): *Alnus* 18 per cent., *Betula* 74 per cent., *Quercus* 4 per cent.; *Corylus* 16 per cent.; *Utricularia* pollen, *Polypodium* and *Tilletia* spores.

Sample 3 (82 cm. below the surface): only 16 *Betula* pollen counted.

The PF is greatest in sample 1 (25), least in sample 3 (8).

It is probable that this moss is of a considerable age. The percentage figures, especially those of alder and hazel, are in favour of the view that the A-zone is contemporaneous with a part of it. If this view is the true one, there cannot have been any rise of land after the Lower Turbarian period, because of the fact, already mentioned, that the moss is situated only about 3 feet above high-water mark. Further, it seems probable that trees or forests once grew in Westray, and that the formation of peat in the moss investigated ceased long ago.

F. *Peat Mosses on the Shetland Islands.*

(Map used: Bartholomew's "Half-inch to the mile" map of Scotland, Sheet 29.)

Before dealing with my own investigations, a brief summary of some of Prof. Lewis's results will be given. According to him the peat appears to be rapidly wasting away over the whole of the mainland; this is particularly marked on the hills in the Wall-Sandness region. The general sequence found over this area is as follows (Lewis, Part II. 1906, p. 50):—

1. *Scirpus cæspitosus*; also *Sphagnum* and *Calluna* (scarce).
2. *Eriophorum vaginatum*.
3. Dense light-coloured structureless peat crowded with the stems of *Calluna*.
4. *Salix Arbuscula*; also *Empetrum nigrum*, *Betula nana*, *Erica Tetralix*.
5. *Betula alba*; *Corylus*.
6. *Sphagnum* and *Eriophorum vaginatum*.
7. *Salix reticulata*, *S. herbacea*; *Betula nana*.
8. *Potamogeton pectinatus*; *Menyanthes trifoliata*, *Viola palustris*, *Ranunculus repens*, *Equisetum* sp.
9. Sand and rock.

Lewis is doubtful whether the aquatic vegetation at the base belongs to the same stage as the Arctic plants immediately overlying it. The aquatic species, however, were only found in a few sections, which renders it probable that they represent small marshy pools which were scattered over the tundra, and therefore actually contemporaneous with the lower layers of creeping

willows found elsewhere in the district. As *Myriophyllum alterniflorum* pollen is often abundant in such silty layers, a careful examination should yield the fruits of this species. Fossil fruits are described by G Anderson, H. A. Weber, and others. In layer 3 the *Calluna* stems were found to be much shrunk; frequently the interior of the stems had disappeared, leaving only the epidermis. As this layer was traced along the banks of streams, it was found to be of unequal thickness. It would appear, therefore, that it marks a period of denudation during which the surface of the bed became wasted and channelled into peat-hags like those met with on the present surface of the moss.

In his Part III. 1907, p. 56, Lewis lays stress upon the circumstance that there must have been considerable climatic changes in postglacial time: "The presence of a buried forest on the west Shetland coast below an Arctic bed shows that the Atlantic cyclones must have pursued an entirely different path when that forest spread over the country, for the most favourable conditions of soil and temperature would not permit forest under present climatic conditions, and indeed a more unfavourable position for tree growth could hardly be found at the present time in North-West Europe."

As to macro-palæontological evidence of the presence of postglacial woodlands in the Shetlands, Lewis found remains (referred to the Lower Forest) of birch, alder, rowan, also of hazel and sweet-gale (iii. p. 52; iv. p. 801). Remains of an Upper Forest were not found. In the Isle of Foula there occurred, however, a juniper-bed, possibly belonging to the Upper Forest; also from the mosses of the Faroe Islands fossil juniper has been described (Ostendfeld, 1901; Jessen and Rasmussen, 1922). Lewis did not meet with macroscopical pine-remains, but he found pine-pollen in a section between Stourborough Hill and Sandness Hill; this occurred in silt with *Equisetum*, which occupied the interstices between the stones at the bottom of the section. He does not consider, however, that these pollen-grains show that pine was ever native in Shetland, because of the distance (in this case "at least many hundred miles") over which pollen may be carried by wind.

In the western part of the Shetland mainland, in the parish of Walls-Sandness, three peat-deposits along the road between Melby and Bridge of Walls were investigated (peat mosses Nos. 24-26), all characterized by the scantiness of fossil-pollen.

PEAT MOSS No. 30.

Situated above 90 m. above sea-level on the watershed, Sound of Papa-Gruting Voe, near point 309 west of Mousavord Loch and a little east of the above-mentioned Sandness road.

Stratification:—

A. 150 cm. *Eriophorum vaginatum* peat; 75 cm. H < 6; then 75 cm. H > 6.

B. 95 cm. *Carex* peat, H 7-8, with *Menyanthes* and large *Equisetum* rhizomes; in places also twigs and rubble swept down by floods and embedded in the peat. The 5 cm. at the bottom resembles a dark clay.

C. Rock.

Analyses:—

- 10 cm. below the surface: 1 *Alnus*; 1 *Ericaceæ* tetrad.
 50 cm. „ „ „ 5 *Ericaceæ* tetrads.
 70 cm. „ „ „ *Ericaceæ* tetrads.
 100 cm. „ „ „ 1 *Alnus*, 3 *Betula*, 1 *Pinus*, 1 *Quercus*.
 150 cm. below the surface: 1 *Alnus*, 7 *Betula*, 17 "*Salix*"; *Ericaceæ* tetrads common.
 200 cm. below the surface: 2 *Alnus*, 13 *Betula* (52 per cent.), 4·5 *Pinus* (18 per cent.), 5·5 *Quercus*; 3 "*Salix*." In this sample occurred many rootlets, probably of *Carex limosa* (cf. Matjuschenko, 1923, fig. 1).

PEAT MOSS No. 31.

A smooth, wet meadow with *Hydrocotyle*, *Juncus squarrosus*, *Montia*, etc., about 150 m. W. of the N.W. point of Lunga Water. It is drained by a curious channel, 60 cm. broad and 120 cm. deep, completely filled by water, in which *Myriophyllum alterniflorum* and *Potamogeton polygonifolius* grow. It was impossible to distinguish different layers, the whole deposit (200 cm.) being of a dy-like character. It rested on a rock-bottom.

Analyses:—

- 45 cm. below the surface: 1 *Alnus*, 10 *Betula*; 4 cf. *Salix*.
 95 cm. „ „ „ 1 *Acer*, 3 *Alnus* (11 per cent.), 18 *Betula* (69 per cent.), 1 *Ilex*, 2 *Quercus*, 1 *Tilia*; 2 *Corylus*; 6 cf. *Salix*.
 145 cm. below the surface: 3 *Alnus*, 10 *Betula* (50 per cent.), 7 *Pinus*; 2 *Corylus*; 24 *Polypodium vulgare* spores.
 195 cm. below the surface: 1 *Betula*, 1·5 *Pinus*, 1 *Quercus*; 24 cf. *Salix*; 1 *Polypodium* spore.

PEAT MOSS No. 32.

A section situated 20 m. S.W. of the Sandness road at the east point of Lunga Water and 6 m. above the level of this loch (about 44 m. above sea-level). Probably it is the same section as that described by Lewis (iv. 1911, pp. 796-797).

Stratification (163 cm.):—

- A. 15 cm. *Calluna* peat.

B. 55 cm. *Eriophorum vaginatum* peat; the upper 15 cm. yellow-brown ($H=4$), with traces of *Calluna*; the lower 40 cm. dark brown; H not reaching 6.

C. 93 cm. *Sphagnum* peat, not quite typical, $H>6$; remains of *E. vaginatum* and *Calluna*.

D. **Rock.**

A sample collected 130 cm. below the surface showed 1 *Alnus*, 2 *Betula*, and 2 *Corylus* pollen-grains; and a sample of the bottom substance, 160 cm. below the surface, 8 *Alnus*, 16 *Betula*, 7.5 *Pinus*, 1 (2?) *Quercus*; 1 *Corylus*. In its pollen character the last sample, in which also 2 *Polypodium* spores were seen, resembles several of the bottom samples already mentioned, e.g. from Wideford Hill (p. 483), Helmsdale (p. 478), and Achnasheen (p. 456).

Among the following peat mosses, the first is situated in the parish of Sandsting, near the Walls-Sandness district; the others are in the middle of the mainland, between Weisdale in the south and Firths Voe in Delting in the north.

PEAT MOSS No. 33. (Text-fig. 17.)

A smooth meadow with drainage dykes, a little W. of Murraster, near the Bridge of Walls-Tresta road, about 20 m. above sea-level (a short description is given in Verh. d. int. Ver. Limnologie, Bd. ii. 1924).

Sequence of layers:—

A. 260 cm. **Magnocaricetum** peat, H 7–8; with *Equisetum* and *Menyanthes*.

B. 170 cm. **Gyttja**, of various tints; at 290–310 cm. below the surface it is yellow-white; 310–360 cm. brownish, with numerous rootlets; 360–400 cm. yellow; 400–420 cm. greenish yellow; 420–430 cm. greenish.

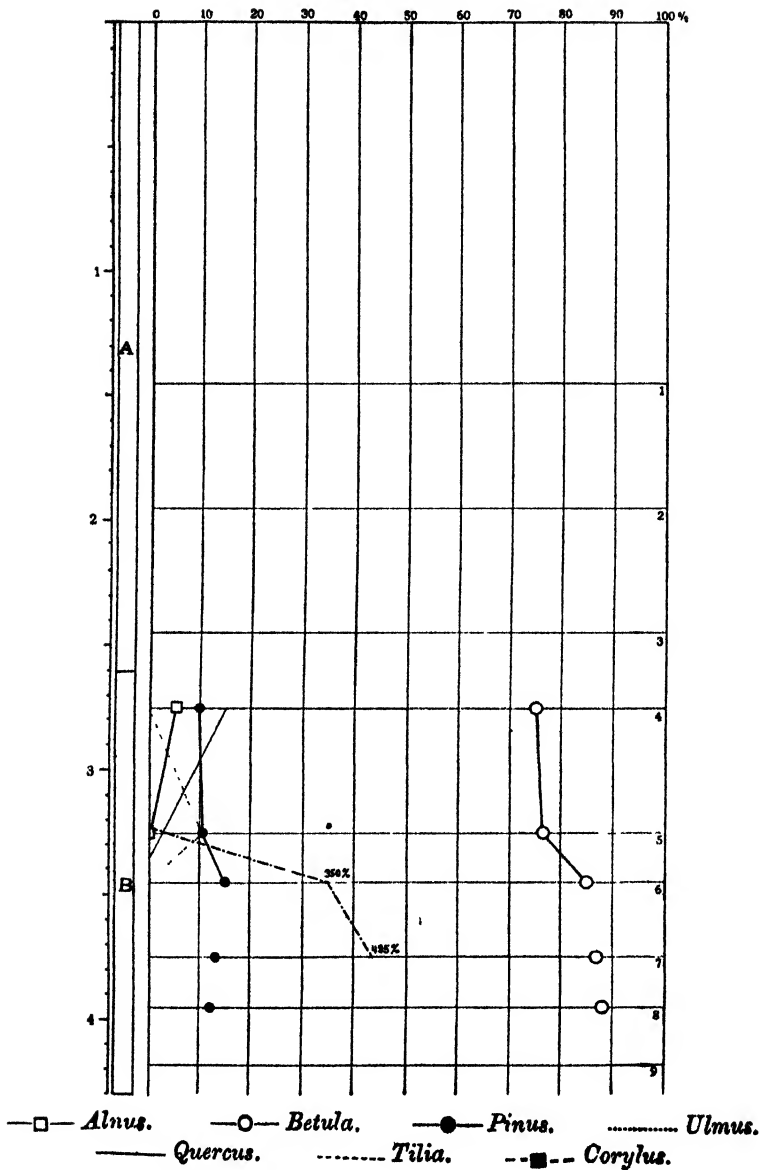
C. **Rock.**

This sequence shows a very low PF, which as to the gyttja is greater in the upper than in the lower part. The percentages for the six samples were calculated when an average of 25 pollen-grains had been counted. Three conclusions can, however, be easily arrived at:—

1. The dominance of birch-pollen.
2. The presence of pine-pollen also in the oldest layers.
3. The pollen of alder, elm, and oak first appear when the upper gyttja-layers are sedimented.

Hairs of *Ceratophyllum* were found in sample 7, and the pollen of *Myriophyllum alterniflorum* attains an enormous frequency (up to 750 per cent.). Also pollen of another species of *Myriophyllum* was seen.

TEXT-FIG. 17.



PEAT MOSS No. 34.

A fairly smooth moss with *Calluna* (dominating), *Erica Tetralix*, *Scirpus cespitosus*, *Eriophorum vaginatum*, and *Sphagnum*, situated in the Tetla Dale. The borings were taken immediately to the E. of the extreme top of Scalla Field, between the stream from Petta Water and the Voe-Sandwater Inn road. Altitude above sea-level about 60 m.

The deposit is 5 m. deep ; at first there is 200 cm. *Eriophorum vaginatum* peat successively passing into a dy-like substance (230 cm.), showing traces both of magnocaricetum peat and of carr peat. Beneath the dy-bed **detritus-gyttja** appears, resting on sand. In the lowest part of the gyttja is a thin layer of sand, 2 cm. thick.

Sample 9 shows a great resemblance to sample 9 from Firths Voe (moss No. 37) ; but if these samples actually are contemporaneous, then, either the formation of peat must have been more rapid in No. 34 than in No. 37, or erosion must have removed parts of the "hill-peat" seen in No. 37 so as to leave the smooth surface of No. 34 intact. Solid wood, which made boring difficult, was found 4 m. beneath the surface, but, curiously enough, the analysis of the sample from this layer resulted only in two pollen-grains, one of pine and one of lime. "*Salix*" pollen has a great frequency, increasing from 40 per cent. in sample 5 to 100 per cent. in 8 and 115 per cent. in 9. *Myriophyllum alterniflorum* pollen occurs in samples 8 and 9 (36, respectively 270 per cent.), and in the same samples also hairs of *Ceratophyllum* have been seen.

PEAT MOSS No. 35.

Calluna-Empetrum moss with *Scirpus cespitosus*, *Erica Tetralix*, *Eriophorum polystachion*, *Airopsis praecox*, *Rhacomitrium*, *Hypnum*, and *Sphagnum* situated at the N.W. point of Petta Water, between the Mid Kame and the Voe-Sandwater Inn road, about 97 m. above sea-level. The section, 265 cm. in depth, chiefly consisted of a *Eriophorum vaginatum* peat-like substance of which the lowest 110 cm. were rich in twigs. In the loch amongst other plants *Myriophyllum alterniflorum* and *Potamogeton polygoniflorus* were seen.

In order to get a control for the distribution of the pollen-grains in different parts of the microscopical preparations, a preparation was made from a sample 53 cm. above the sandy base of this moss, and examined as follows:—The number of pollen-grains was calculated separately for consecutive sections of the preparation analysed. The area of each section was 26·24 sq. mm. (= 32 × 0·82 mm. = the product of the length of the cover-glass and the diameter of the field of vision. Optical apparatus: a compensating eyepiece No. 6 and an apochromatic objective 8 mm.).

	<i>Alnus.</i>	<i>Betula.</i>	<i>Quercus.</i>	<i>Ulmus.</i>	<i>Corylus.</i>	" <i>Salix</i> ."
Section 1	2	31	—	1	—	3
" 2	—	27	—	—	—	2
" 3	—	19	1	1	—	4
" 4	1	24	—	—	1	3
" 5	1	21	—	—	1	—
Total	4	122	1	2	2	12
Percentage ..	3	95·5	trace	1·5	(1·5)	(9)

This table shows the homogeneity of the different parts of a preparation, as was shown by von Post (1916) and the author (1921, p. 21, also as quoted by Docturowsky, 1923).

The lowest sample (261 cm. below the surface) contained, unlike that just mentioned, 6 pine-pollen grains (20 per cent.) ; also 19 *Betula* (63 per cent.), 3 *Quercus*, 3 *Corylus*, 7 cf. *Salix* and 1 cf. *Alnus*. Thus the moss must be younger than mosses such as Nos. 34 and 36.

PEAT MOSS No. 36.

Situated at the south border of Voe Loch (117 feet above sea-level), between the loch and the Voe-Lunna road. Depth of the deposit 147 cm. A sample 7 cm. above the sand-bottom exhibited the following pollen-spectrum: *Alnus* 30 per cent., *Betula* 60 per cent., *Pinus* 3.3 per cent., *Quercus* 1.7 per cent., *Ulmus* 5 per cent.; *Corylus* 15 per cent., cf. *Salix* 50 per cent. PF=40.

PEAT MOSS No. 37.

A deposit, 262 cm. thick, resting on rock situated in the dale of Sandgarth Burn south of Dales Voe, due west of the road between Wester Scord and Djüpa Gill. A sample was taken from the highly-decayed base (260–262 cm. below the surface). The analysis showed 3 alder, 4 birch, 8 pine, and 2 hazel pollen-grains (representing respectively 20 per cent., 27 per cent., 53 per cent., and 13 per cent.).

PEAT MOSS No. 38. (Text-fig. 18.)

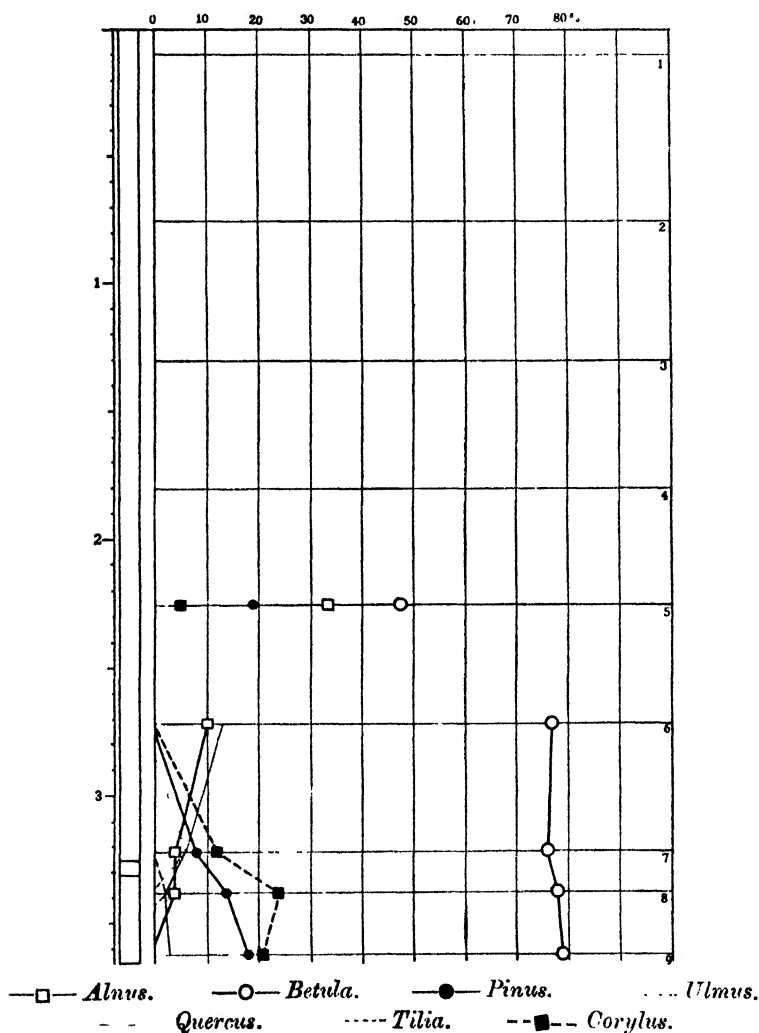
In order to get a representative example of the "hill-peat," which covers the greater part of the Shetland kames and hummocks to a depth of 3 m. or occasionally 4 m., a series was collected from the wall of a peat-bag newly dug in the neighbourhood of Firths Voe. It lies immediately S. of the road which is a little to the W. of Firths Voe and near the stream from Sand Water and Bordigarth Loch. This deposit is the most northerly one investigated. The exposure had a depth of 180 cm.; below this specimens were obtained with the bore, the rock-bottom being at a depth of 365 cm. beneath the surface.

The peat was much decayed, a yellow-brown strip of *Sphagnum* peat (65–75 cm. below the surface) excepted. The lowest part contained many twigs; the layers immediately above the base were dark, probably very compressed and difficult to bore. 325–331 cm. beneath the surface was a layer of grey sand.

The diagram exhibits clearly the decrease of the pollen frequency from the base (PF=5–7) to the upper layers (PF=0). The great amount of *Corylus* pollen in the 3 lowest samples is interesting as a parallel to features already mentioned from the Hebrides, the Orkneys, and Ross. In sample 8

a lime-pollen grain was found, and there seem to be several reasons why this layer should be referred to the A-zone (behaviour of alder- and pine-pollen etc.). The importance of the *Salix* vegetation in older times is shown by the percentage figures from samples 5-9, which are respectively 478, 35, 184, 162, and 273 per cent. These figures, however, must not be interpreted as

TEXT-FIG. 18.



showing that the *Salices* had their maximum occurrence during that stage of the formation of peat represented by sample 5 (478 per cent. "*Salix*"). This dominance is only relative. It might be caused by the gradual decrease and disappearance of the Shetland forest trees.

West of this peat moss on the shore of Garths Voe, N.W. of Laxobigging, is a salt meadow, the vegetation consisting only of *Plantago maritima*. A sample taken from highly-decayed dy-like substance 65 cm. below the surface showed *Alnus* 0.75 per cent., *Betula* 96.5 per cent., *Pinus* 2 per cent. *Quercus* 0.75 per cent.; *Corylus* 1.5 per cent.; "*Salix*" 59 per cent. The excessively high pollen-frequency (304) is noteworthy. It is clearly the result of two factors: a local *Betuletum* and an exceedingly slow growth of peat.

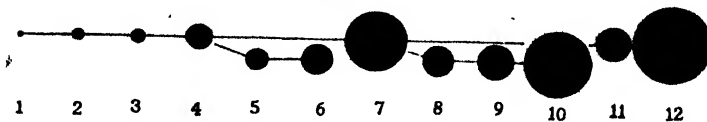
3. THE POLLEN FREQUENCY (PF) IN THE PEAT MOSSES INVESTIGATED.

In 'Geologiska Föreningens Förhandlingar,' Bd. 45, 1923, is a brief account of the pollen frequency in the Scottish deposits. It must be emphasised that the figures here published cannot be regarded as exact. Nevertheless they have a certain interest. For sedentary material the following pollen-frequency numbers have been obtained:—

<i>The Shetlands</i>	8.2	(text-fig. 19, 2)
<i>The Orkneys</i>	12	(„ 19, 3)
<i>The Hebrides</i>	33	(„ 19, 4)
Isle of Lewis	25	(„ 19, 5)
Isle of Skye	51	(„ 19, 6)
<i>Ross and Sutherland</i>	192	(„ 19, 7)
Helmsdale	51	(„ 19, 8)
Strathcarron ...	73	(„ 19, 9)
Achnasheen	269	(„ 19, 10)
<i>N. Scotland and the Isles</i>	70.4	(„ 19, 11)
[<i>N.W. Germany</i> (Erdtman, 1924). 335	(„ 19, 12)]	

The area of the circles in text-fig. 19 is proportional to the numbers giving the pollen frequency. There is also a circle, almost a point, which gives an idea of the PF of the Faroes (text-fig. 19, 1). The number (PF=0.34), which

TEXT-FIG. 19.



is calculated from the table (p. 19) in the paper by Jessen and Rasmussen (1922), is not to be compared strictly with the figures from Scotland, because Jessen, who made the Faroe analyses, may perhaps have made preparations of a different thickness from those made by the author.

Von Post (1916) and Hesselman (1916) have pointed out the desirability of making PF calculations based on a unit of volume, and the latter has given a short description of the manner in which this may be done. Prof. Lagerheim has kindly drawn my attention to a paper by A. Meyer (1908), describing

a quantitative method for microscopical analysis. But the methods involve great expenditure of time, and even then the resulting numbers are not quite comparable, because of the varying rate at which peat forms.

As to the Faroes, it must be remarked that the above-mentioned PF figure is based upon a single peat moss only, from which 7 specimens were collected for microscopical analysis.

It has been mentioned that in the upper layers of the peat deposits, especially those of the Shetlands, Orkneys, and Lewis, tree pollen is practically absent. When the pollen-flora of Scottish deposits has been more thoroughly explored, it would be a fascinating occupation to compare these changes in the pollen frequency with the state of woodlands in old times, as described by historiographers such as Herodian, Solinus, Tacitus, Torfæus, and others.

Where absolute frequency figures are lacking, relative ones have often been used. For instance, it has been stated by several authors (*e.g.* Sandegren, 1916, and von Post, 1916) that the PF in most cases is greater in highly-decayed than in slightly-decayed peat. To express the degree of humification, von Post used a scale of 10 divisions, 10 being the highest (*cf.* p. 4). Sandegren (*l.c.*), using von Post's scale, obtained:—from a layer of pre-subatlantic *Sphagnum*-peat with humification represented by 9, a $PF=34.5$; from layers with humification 8 and 7, respectively, $PF's=25$ and 17 ; from subatlantic peat with humification 3 or 2, as well as from slightly-decayed pre-subatlantic peat, $PF=7.5$ (these figures are calculated upon those of Sandegren, who expressed the PF as the mean number of pollen-grains per preparation, 18×18 mm.; the relatively low figures indicate that he used preparations much thinner than those used by the author).

Other suggestions as to the PF might be obtained from Halden, 1922 and Auer, 1923. The former (*l.c.* fig. 5, p. 21) figures a PF curve from a deposit with a postglacial marine-clay bed situated between two peat strata. When compared with other curves, this PF curve serves to show the layer of the marine clay which must have been formed when the land-surface was at its lowest level. The latter (*l.c.* fig. 66, p. 218) gives a diagram illustrating the PF for different kinds of peat in different stages of decay.

4. THE FOREST TREES. *A Summary of the Occurrence of their Pollen-grains in the Deposits investigated, and a Comparison with the Occurrence of Pollen in the Peat Mosses of Sjælland* and S.W. Sweden*.*

1. **Acer.** Maple-pollen is exceedingly rare, only half-a-dozen pollen-grains having been counted from the Shetlands, Orkneys, Hebrides, and Strathcarron (Ross). Its behaviour is exactly the same in Sjælland (Jessen, *l.c.* p. 187, and S.W. Sweden (Erdtman, *l.c.*; Halden, 1922, p. 13).

* According to Jessen, 1920, and Erdtman, 1921.

2. *Alnus*. In Finland, Norway, and Sweden the zone where the regular appearance of the *Picea* pollen begins is often used as a valuable standard zone (*cf.* the papers of von Post, Holmsen, Auer 1923, Malmström 1923, etc.). This standard zone cannot be employed either along the S.W. coast of Sweden, where spontaneous *Picea* is absent, or in Scotland, where no *Picea* pollen has been found. In Sweden the zone showing the first appearance of elm-, lime-, and oak-pollen is sometimes very characteristic, and has been used as a standard zone by Sandegren (1916). In Scotland, however, the scanty and irregular appearance of the pollen of these three species does not permit of such a use. Instead, the zone at, or a little above, the first appearance of alder-pollen—the “A-zone”—seems to be the niveau best fitted for the comparison of different deposits. If further investigations be carried out, it might become possible to draw maps showing the distribution of peat mosses (and the character of the forests) at different periods. The pollen-diagrams here published make it probable that the peat deposits covered a much smaller area before the A-zone period than they do now. In Sjøælland and Sweden the first alder-pollen appears in late boreal strata (about 6000 years B.C.), and it is probably the same in Scotland.

When an alder wood grew on the surface of a peat moss, its presence is usually indicated by a great amount of alder-pollen in the peat. It is in this way that the highest percentages of alder are to be explained (*e.g.* 58 per cent.; peat moss No. 4). The moors in the neighbourhood of Strathcarron (mean percentage=27, maximum=49 per cent.) and Helmsdale show a greater alder-pollen frequency than the Achnasheen district and the Isles. The Shetland deposits and especially those of Lewis are very poor in alder-pollen (mean frequency 6–8 per cent.).

The pollen of *Alnus glutinosa* and *A. incana* is indistinguishable, but in Scotland the pollen must belong exclusively to the former species.

3. *Betula*. As in *Alnus*, the pollen of the different species is scarcely distinguishable. According to Docturowsky and Kudrjaschow (1923, figs. 13–15) there is a difference in the size between *Betula humilis*, *B. alba*, and *B. nana*, but from preparations made by myself I find it quite impossible to distinguish between them, certainly not between the two latter species.

In no part of Europe which has so far been investigated by the statistical method of pollen research, has such an overwhelming dominance of birch-pollen been found as in Scotland. Birch was the first tree which invaded the country in postglacial time. It is not improbable that in places it was accompanied by pine (aspen, rowan, etc., cannot be considered, as the pollen of these is not preserved in peat or mud). Along the coast of S.W. Sweden, birch-pollen is always dominant in the oldest (pre-boreal) layers. Most frequently it is also dominant in late sub-boreal strata and in the subatlantic *Sphagnum* peat, the surface-layer excepted.

4. **Carpinus**. Only two pollen-grains from Orkney deposits have been identified with certainty as belonging to the hornbeam. Only small quantities of the pollen of this tree have been recorded in Sjælland and S.W. Sweden, showing that its immigration occurred during the sub-boreal period.

5. **Corylus**. Although not a forest tree *sensu stricto* it will be briefly considered here. The highest frequency for hazel-pollen is found about the A-zone. Also in Sweden it has its maximum occurrence in very old (boreal) layers, a subject studied very thoroughly by von Post (1916). It is probable that this behaviour will prove to be a salient feature in the mosses of North and Middle Europe (*cf. e. g.* Rudolf and Firbas, 1923; Stark, 1923).

6. **Fagus**. Only 3 pollen-grains were met with: 1 from Shetland, 1 the Orkneys, and 1 from Lewis.

(6*b*. **Fraxinus**. Pollen resembling that of *Fraxinus* was seen, but the determination was uncertain.)

7. **Ilex**. Pollen-grains, in all 5, were obtained from the same places as the beech-pollen.

8. **Pinus**. It is a most striking fact that pine-pollen occurs in practically all samples in which birch-pollen occurs. In the oldest part of the Shawbost gyttja (Lewis) birch-pollen is lacking and pine-pollen too. It is possible, however, that much of the pollen may have been transported a great distance by the wind, and that in consequence we have no reliable evidence as to the distribution of pine in the earliest postglacial times. At the A-zone period the great percentage of pine-pollen, the presence of fragments of leaf epidermis, and in places of great trunks and stools, prove that pine grew in Ross-shire. High pollen-percentages from the Outer Hebrides (46, 32, 30 per cent., etc.) make it very probable that pine also grew there at the same time. J. Geikie (1867) tells of pine-remains from these islands, but without definite description of the localities. As the A-zone seems to be of a very considerable age—I think it is most probable that it should be correlated with the boreal of the Scandinavian peat-geologists—pine forests must have covered parts of Scotland at a much earlier time than Lewis and Samuelsson have suggested.

As to the Shetlands, the mean pine-pollen percentage is 10 (the figure may not be quite reliable owing to the scantiness of pollen in the samples analysed). No macro-remains have been found, and the question as to the indigenous occurrence of pine in Shetland must be left unsolved. Curiously enough, the only account which I have seen of pine-remains from the Shetlands is published in the 'Transactions of the New Zealand Institute' (Speight, 1911). The account must, however, be a mistake.

Both in S.W. Sweden and Sjælland pine-pollen has been found in old pre-boreal gyttjas. As in Scotland, so here, birch-pollen is dominant, but a definite birch-aspen period is not clearly to be distinguished.

9. *Quercus*. Oak-pollen, which plays an important part in the pollen-flora of S. Sweden, N.W. Germany, etc., exhibits no interesting features in Scotland. It occurs to about the same extent (2-5 per cent.) in all the districts investigated. Above the A-zone it usually has a greater percentage than elm-pollen, below it elm-pollen is the most frequent. Only very rarely are percentages up to 10, 15, or 20 met with. In Denmark and Sweden oak-pollen is found belonging to the oldest Neolithic Age.

10. *Tilia*. 9 pollen-grains were found: 4 from Achnasheen, 3 from the Shetlands, 1 from Skye, 1 from Helmsdale. Jessen and Rasmussen (1922) found 1 lime-pollen grain in the Faroes. In Sjælland and Sweden it occurs much more abundantly. Its first appearance, as that of the elm, dates from late boreal time ("the Mullerup period").

11. *Ulmus*. Elm-pollen has the same occurrence as oak-pollen, but its highest percentage occurs at an earlier period than that of the oak. Its mean frequency is exactly half that of the oak. In the peat mosses of South and Middle Sweden the frequency is greater, but only in exceptional cases does the percentage reach 15 and up to 36 (*cf.* Halden, 1917, p. 143).

5. THE CHARACTER OF THE POSTGLACIAL WOODLANDS OF SCOTLAND AND SOME OTHER COUNTRIES AS SUGGESTED BY THE STATISTICAL METHOD OF POLLEN RESEARCH.

If the sum of all pollen-grains (14,843) recorded in the above analyses is taken, and the percentages of the different species of pollen is then calculated, we get a sort of general pollen-spectrum giving us an idea of the forest character of N. Scotland and the Isles in postglacial times. The percentage figures are as follows:—

Betula 70 per cent.

Pinus 14.6 per cent.

Alnus 11.8 per cent.

Quercus 2.4 per cent.

Ulmus 1.2 per cent.

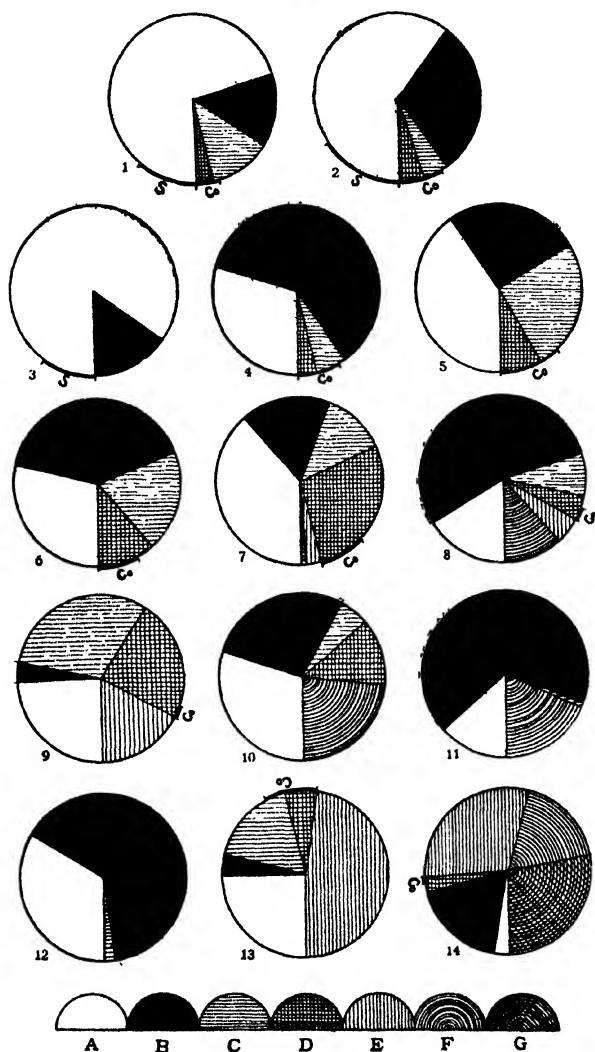
Acer, *Carpinus*, *Fagus*, *Fraxinus*?, *Ilex*, *Tilia* only traces.

(*Corylus* 4.25 per cent.)

("Salix" 11.25 per cent.)

This spectrum is shown diagrammatically in text-fig. 20, and for comparison the general spectrum of the A-zone is shown in No. 2. These diagrams for several reasons, however, are only very approximate. We do not know, for instance, with the accuracy that could be desired, how the area of the pollen-producing forests reacts upon, and is related to, the fossil pollen-flora. A first attempt to solve this question by direct observation was made by the author (1921). The forests in a district of

TEXT-FIG. 20.



POLLEN-SPECTRA.

- | | |
|----------------------------------|---------------------------------------|
| 1. Scotland (general spectrum). | 8. Holland (S.W. Sweden) |
| 2. " (spectrum of the A niveau). | (late subatlantic spectrum). |
| 3. Holland (S.W. Sweden) | 9. N.W. Germany (Bremen). |
| (pre-boreal spectrum). | 10. Rodkino, Tver (Russia). |
| 4. " (late boreal "). | 11. Finland ("abiegn" time). |
| 5. " (Atlantic "). | 12. " ("pre-abiegn" time). |
| 6. " (sub-boreal "). | 13. N.E. Sjælland, Denmark. |
| 7. " (subatlantic "). | 14. Sebastiansberger Heide (Bohemia). |

A = *Betula*; B = *Pinus*; C = *Alnus*; D = Mixed oak forest (*Tilia*, *Quercus*, *Ulmus*, etc.); E = *Fagus* + *Carpinus*; F = *Picea*; G = *Abies*; S = *Salix*; Co = *Corylus* (percentage calculated separately).

S.W. Sweden were mapped, and comparisons made with the recent or sub-recent pollen-flora of the same district.

Text-fig. 20, Nos. 3 to 8 show the mean pollen-spectra of that district at different periods [No. 3: pre-boreal spectrum (niveau 89); No. 4: late boreal do. (niveau 61); No. 5: Atlantic do. (niveau 55); No. 6: sub-boreal do. (niveau 39); No. 8: subatlantic do. (niveau 11); No. 7: late subatlantic do. (niveau 3)]. The striking resemblance between No. 4 (late boreal spectrum) and No. 3 (the A-zone of Scotland) is to be noticed. *Salix* and *Corylus* pollen are calculated separately. The percentage of the latter is greater in Nos. 4 and 5 and smaller in Nos. 6, 7, and 8 than that of the mixed oak forest (elm, oak, lime). Because comparisons can easily be made, a great number of characteristic zones have been distinguished, each of which is marked by a special number. The above numbers (89, 61, 55, etc.) refer to these different zones. Von Post has made investigations, upon a large scale, of peat mosses in the whole middle and south of Sweden. The results of these were recorded in a paper read at the congress of Scandinavian naturalists at Gothenburg in the summer of 1923 (published in Geol. Fören. Förhandl. March 1924). Further diagrams from more northern parts of Sweden (Helsingland) will be found in the paper by Halden, already mentioned (Halden, 1917), and the paper of Malmström (1923). The diagrams of the former are not directly comparable with those of von Post, as the alder-pollen is calculated separately. Malmström's diagrams (l. c. p. 148) show, among others, important percentages of *Picea* pollen.

No. 10 shows the subatlantic spectrum from two high moors in N.W. Germany (Grienenwaldmoor an Borner Moor in the neighbourhood of Bremen). *Alnus* is unquestionably the dominant pollen, and this dominance extends also to the greatest part of the pre-subatlantic strata.

No. 9 illustrates a general spectrum from a peat moss near Redkino, Government of Tver, Russia. It has been constructed by reference to a diagram published by Gerassimoff (1923, fig. 6, 1, p. 32). It is possible that the oldest postglacial strata are wanting.

Nos. 11 and 12, based upon the diagrams of figs. 72, 74, and 76 in Auer (1923), show mean pollen-spectra from northern Finland; the former gives an idea of the forest conditions after, the latter of the conditions before, the immigration of the spruce (the "abiegn" and "pre-abiegn" times respectively*). As to the deciduous trees, Auer has only counted the pollen frequency of alder and birch, other species being of very little importance.

Rudolph and Firbas (1923) were the first to publish a pollen-diagram from a country south of the Baltic. No. 13 illustrates the subatlantic part of their diagram from the "Sebastiansberger Heide" (Erzgebirge, Bohemia).

* These terms are not good, as they cannot be used in the same sense in all countries where *Abies* occurs.

In striking contrast to this spectrum is No. 14 from North-East Sjælland ; it, too, shows a subatlantic spectrum. It is based upon the diagrams given by Jessen (1920) from Sækkedam, Warming's Mose, and Maglemose. The only feature in common with the diagram from Sebastiansberger Heide is the large percentage of *Fagus* and the small percentage of the mixed oak forest.

6. SUGGESTIONS FOR A PROGRAMME FOR FURTHER INVESTIGATIONS.

Great Britain and Ireland offer a large and advantageous field for continued researches in the statistical method. In his 'Origin of the British Flora,' C. Reid has collected the facts as to pre-, inter-, and post-glacial floras published before the year 1900. Although much more information has been accumulated during the last twenty-five years, many problems, especially those relating to the age of deposits, still remain unsolved (*cf.* Bennie, 1891, the Redhall flora from a section described by Henderson in 1874 and many others).

A comparison is greatly to be desired between the micropalæontology of the interglacial beds of Great Britain and those of Middle and Eastern Europe. These latter have, especially as to macro-fossils, yielded much of great importance. Quite recently A. Kozłowska (1923) has discovered (at Rakow, Poland) wood-remains which can hardly belong to any other species than *Tsuga canadensis*. Pollen-diagrams from such places would be of much value for the comparison of deposits.

Pollen-spectra from the spruce-bearing strata of the Cromer Forest Bed might be of special interest (*cf.* C. Reid, 1880, 1900, 1913 ; C. and E. M. Reid, 1907-1909).

By the use of the statistical method in a more or less modified form, we might also study material older than these late Pliocene strata, *e.g.* the brown coal, from which Gümbel (1883) in an extensive paper has described and figured pollen which occurred abundantly ; also epidermal fragments of grasses, conifer needles, diatoms, spicules of Spongillæ, etc. (*cf.* also Bertrand (1913).

Gümbel (*l. c.*) and Reinsch (several papers, 1881-1883), and most recently Turner and Randell (1923), have also given an account of the micropalæontology of coal from Trias, Dyas, Permian, and Carboniferous strata. Reinsch has described under the collective name *Trilites* small bodies closely resembling *Sphagnum* spores. That these sometimes occur in extraordinary profusion appears from the following passage from a paper of 1887:—
 " Mehrere dieser *Trilites*-formen im Russischen Carbon finden sich in solch enormer Menge, dass man den Antheil dieser mikroskopischen Körper an der Substanz wohl zu 80-90 per cent. annehmen kann. Von der erdigen und Torbanitähnlichen Steinkohle von der Pruckscha Guvern. Nowgorod wird ein Cubikcentimeter ungefähr 5,827,000 einzelne *Trilites*-körper von durchschnittlich 0.033 mm. diam. enthalten."

When studying the postglacial deposits, reference should be made in as many cases as possible to archæology, and to geological features such as the rise and fall of land. Flint implements are found in great numbers in or below peat layers, also remains of Roman roads (*cf.* Moss, 1904, pp. 663–664 *). Currie (1869) has given an historical résumé of the occurrence of canoes buried in the bed of the Clyde and in lakes and marshes in the out-lying islands. Submerged postglacial peat is found around the coasts of Great Britain, and especially on the east coast of Ireland (*cf.* Close, 1878, p. 75). Also the study of peat between the mean high-water level and the lowest raised beach is of interest.

From such places as could be dated by archæology or geology a series of specimens should be taken for analysis. Then correlations should be carried out between one moor and another, most appropriately along lines drawn across the whole country. Taking these as a basis, it would then be easy to examine and date other deposits whose age it was desired to know.

Also calcareous tufa could be investigated (*cf.* Holmsen, 1920). A deposit of this kind was described by C. Reid (1897), and an especially interesting one, resting on peat, by Maw (1866).

Besides pollen-grains, other micro-fossils could be studied, for example the rhizopods, with the study of which Dr. Harmsch, Breslau, is occupied. Wright (1896) has also written a paper dealing with research methods in connection with foraminifera. Halden (1922, p. 19) has published a biological-bathymetrical diatom diagram from the Lunna moss in S.W. Sweden, and a combined diatom-pollen diagram from the same moss (p. 21). When such combinations can be made, they naturally contribute to the more exact knowledge of the locality studied. *

Before I close, I would express a wish that within the next few years there might be compiled, by the aid of international co-operation, a text-book of peat-palæontology, including both macro- and micro-fossils. The few papers hitherto published are very scattered; and, in consequence, the amount of work which must be undertaken by anyone wishing to study peat has been rendered unnecessarily heavy.

* Moss is of the opinion that the peat moors of the Pennines cannot be considered older than 2000 years, probably dating from the Roman Conquest. In some places the deposits may be of this age; where, for instance, the remains of the Roman roads do not lie in the peat, but on the subsoil. In other places I think they will prove to be of the same age as many of the old Scottish peat mosses.

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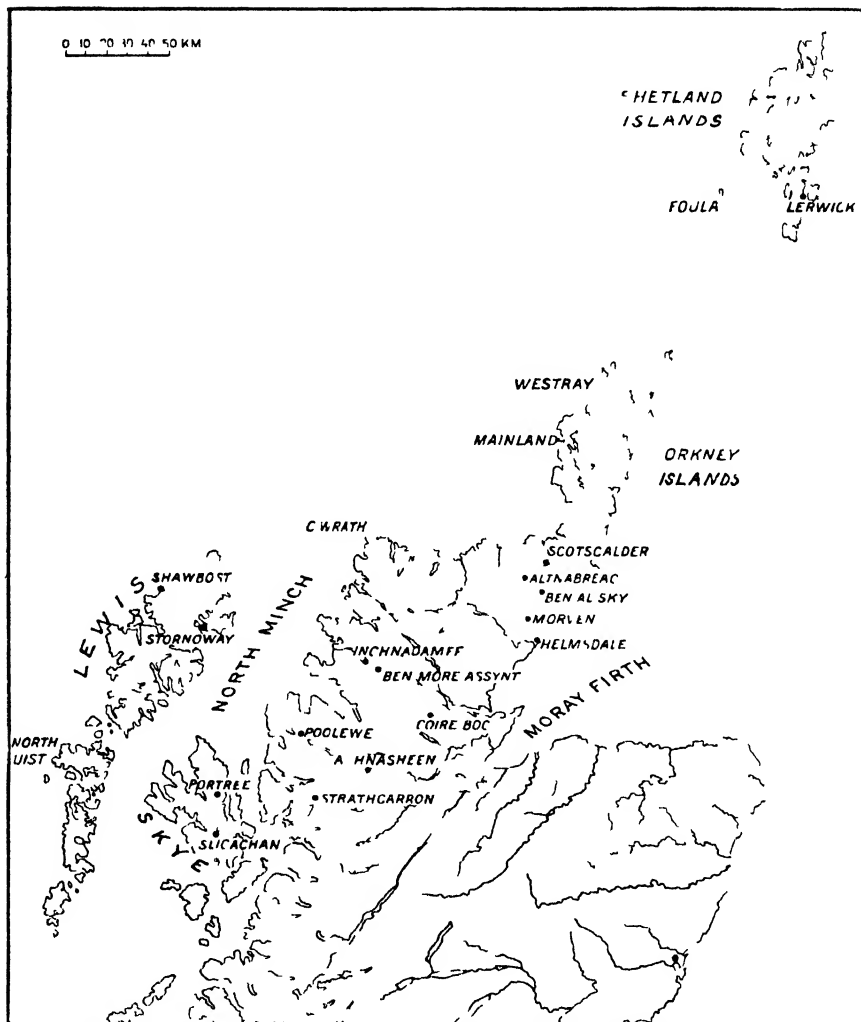
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EXPLANATION OF PLATE 41.

Map illustrating the region investigated.



PEAT MOSSES INVESTIGATED

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[Synonyms are printed in *italics*. A star * denotes the first publication of a name, and a dagger † denotes a fossil plant.]

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